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STUDIES IN THE DISTRIBUTION OF INSECTS BY AERIAL CURRENTS

EXPERIMENTS IN AERIAL TOW-NETTING FROM KITES

BY A. C. HARDY AND P. S. MILNE

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(*With Plates* 8–10 *and* 15 *Figures in the Text*)

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1. INTRODUCTION

DEFINITE migrations are made by a number of the larger flying insects, notably Lepidoptera. Williams (1930), in addition to his own observations, gives a full bibliography of earlier references to insect migration, and recently a study of the migrants into this country has been pursued by the South-Eastern Union of Scientific Societies under the energetic leadership of Capt. T. Dannreuther, R.N., and reported in the *Entomologist* from 1933 onwards. But it is also clear that many of the smaller species must be carried passively by aerial currents: both vertically by convection or other disturbances and horizontally by wind. One of the present authors remembers Mr E. R. Speyer emphasizing the importance of wind drift in the dispersal of the aphid *Chermes* and suggesting in 1920 the tow-netting of the air from aeroplanes. Felt (1925*a*, 1925*b*, 1926, 1928) has discussed such influences at length and collected a large number of examples. Elton (1925) described vast numbers of the aphid *Dilachnus piceae* Panz., and the hover-fly *Syrphus ribesii* Linn. carried on to the ice-cap of North-East Land apparently from the Kola Peninsula, a distance of over 800 miles in a straight line. Uvarov (1931) further discusses the influence of

wind on distribution in his important review of previous work on insects in relation to climate.

The first collections of insects from aeroplanes appear to have been made in America by Coad (1931), who reports on the use of collecting traps up to the height of 14,000 ft.[1] In the following year further experiments in America were made by Collins & Baker (1934).

Travellers at sea have on occasions noticed numbers of insects carried to their vessel when many miles from land. Such an experience one of us (A. C. H.) had on the voyage of the R.R.S. *Discovery* in the autumn of 1925, when a hot wind brought hundreds of insects, large and small, on to the ship from the west coast of Africa more than a hundred miles away.

The following notes are taken from a diary with the midday position of the ship for the dates concerned: 26 October 1925 (16° 23′ 20″ N.; 18° 27′ 15″ W., 130 miles from the African coast): "More insects have come on board to-day than ever before: several butterflies, numbers of moths and beetles and countless grasshoppers, locusts and flying bugs. The latter were a perfect pest, appearing everywhere."

On 13 October (35° 50′ N.; 13° 48′ W., i.e. 310 miles from Portugal and 340 miles from Morocco) I recorded "Spurge hawk moth or allied species, Silver 'Y' moth, other moths and a red admiral butterfly" having come on board; and on 15 October (31° 55′ 30″ N.; 14° 50′ 10″ W., i.e. 295 miles from the African coast) a death's head hawk moth was taken on board.

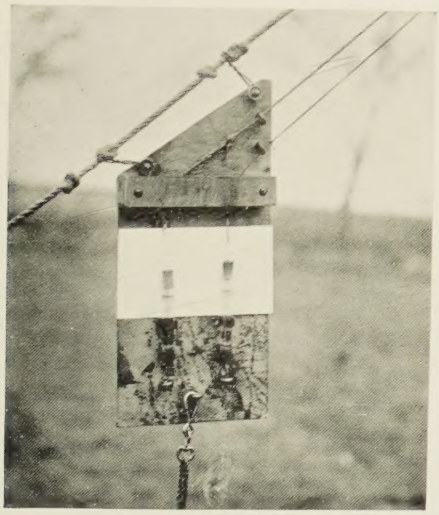
This occurrence at the time when we were engaged in studying the drifting life of the sea, the plankton, led to the development of the methods about to be described; they are an adaptation of oceanographical technique to the study of the "aerial plankton". The process is inverted in the air by sending up kites to support the nets which are opened at the desired height and then closed again before being hauled down, thus ensuring a correct estimation of the small insects drifting at any particular height.

The experiments were begun in May 1932 and continued through the summers of 1933, 1934 and 1935. The senior author (A. C. H.) wishes to make it clear that whilst he directed the experiments and took part in the treatment of the data obtained, the second author (P. S. M.) carried out the greater part of the work in the field and was entirely responsible for the sorting of the collections. The field work in 1935 was carried out by Mr J. A. Freeman who has kindly allowed us to incorporate the material he collected, and will himself contribute a subsequent paper dealing with a more intensive study of insect drift at lower levels which he made in the same year by using collecting nets on the tall masts of a wireless station.

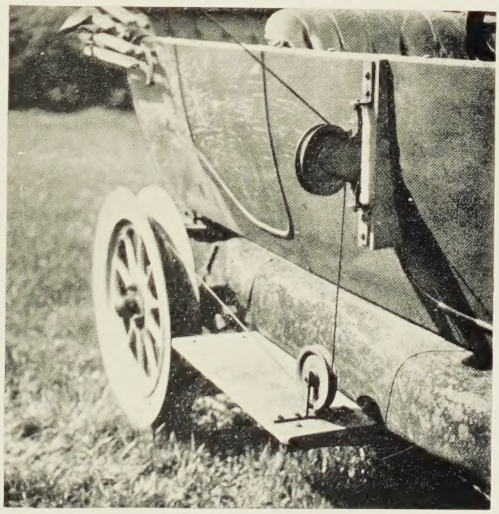
We are indebted to the Agricultural Research Council for a grant of £100 towards the cost of the investigations in 1933. In 1934 and 1935 the work was continued when the second author and Mr Freeman held Ministry of Agriculture Research Scholarships. A brief account of the experiments was given

[1] See Addendum note on p. 226.

Phot. 1. Net going up closed.



Phot. 2. Detail of opening and closing mechanism.



Phot. 3. Kite line leading from spare wheel of car adapted as power winch.

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at the Leicester meeting of the British Association for the Advancement of Science (Milne, 1933) and in the Ministry of Agriculture's *Report on the work of Agricultural Research Institutes* 1932–3 (1934).

Further experiments from aeroplanes using tow-nets instead of traps were begun in France in the summer of 1934 by Berland (1934, 1935, 1936).

The researches described in the present communication form the beginning of a series of investigations, which will form the subject of later papers, on the distribution of insects by aerial currents. A preliminary account of insect drift over the North Sea has already appeared (Hardy & Milne, 1937). During the summers of 1936 and 1937 trial experiments were made with collecting devices on railway trains to obtain series of consecutive samples of insects across the country with a view to investigating the spread of agricultural pests under different weather conditions and the possibility of eventually forecasting such movements.

2. ACKNOWLEDGEMENTS

We have been most fortunate in securing the kind co-operation of a number of specialists in the identification of our specimens. We are most grateful to Mr N. D. Riley, Keeper of Entomology at the British Museum (Natural History), for his kind interest in this work and to the members of his staff who so generously gave their time to the examination of sections of our collections as follows: Dr K. G. Blair (Coleoptera); Mr W. E. China (Hemiptera, excluding Aphididae); Dr F. W. Edwards (Diptera); Dr G. Ferrière (Hymenoptera).

The naming of Aphididae was undertaken by the second author (P. S. M.) after receiving valuable instruction in methods at the Museum from Mr Laing, who also confirmed his identifications and named some others. Mr E. R. Speyer kindly identified the Thysanoptera, Mr G. J. Kerrich of Cambridge two specimens of Hymenoptera, *Gyrocampa affinis* Nees. and *Hemiteles necator* Grav., and Mr J. V. Pearman a specimen of the psocid *Pterodela pedicularia* Linn.

To all these gentlemen we tender our most grateful thanks.

3. EQUIPMENT

Kites, wire and winch

Except in high winds the net is taken up by two kites flown in series. The first is a pilot kite of triangular section box pattern with side wings, having a span of 8 ft. and a height of 8·5 ft. One of similar design but smaller is shown at the top of phot. 5 in Pl. 9. It is easily started in quite light winds and flies very steadily at a good angle. It is connected by 350 ft. of rope to the back of the main lifting kite which is of a double triangular box pattern (see Pl. 9, phot. 4) and specially suitable for use with a pilot. This is 8 ft. across and 5·5 ft. high. About 8 ft. below it are attached the net and its control mechanisms.

This arrangement gives very good results with winds up to force 6 on the Beaufort scale. The two kites, being separated by 350 ft. of rope, combine to smooth out the effects of minor irregularities in the wind and so give a nearly constant angle of pull; whilst the lower kite is experiencing a lull the pilot, further to leeward, may be pulling strongly and so helping to maintain its fellow till the next gust arrives. Longer period variations in the wind velocity cause a slow rising and falling of the whole system which can be overcome to some extent by veering out or hauling in at the right moments.

With winds of force 6 and upwards the pull of the two kites becomes dangerously strong and the pilot kite may be used alone. This eliminates the risk of a breakaway, but the stability of the system is much reduced.

From the net downwards steel piano-wire, $\frac{1}{32}$ in. diameter, is used; it combines the advantages of low wind resistance, light weight (16 lb. per mile length) and high tensile strength, and may be obtained in continuous lengths of a mile or more. The rope and wire are connected by a Dines shackle. Care must be taken to keep the wire well oiled and free from kinks. We have been much helped by consulting Dines' (1903, 1909) accounts of his pioneer meteorological kite investigations, and by receiving valuable advice from his son, Mr J. S. Dines, of the Meteorological Office.

An old Morris Cowley touring car was converted into a simple and convenient power winch. A spare wheel was made into a storage and winding drum, by welding deep flanges on to the rim; it proved sufficiently strong to withstand the strain of more than a mile of wire wound on under tension. The car, which carries all the apparatus to the scene of operations, is run into a position at right angles to the wind, the rear axle is jacked up at one side and the drum substituted for the off-side wheel. Two pulleys, one fixed and the other free to swing through 180° (see Pl. 8, phot. 3), lead the wire out to the kites.

The kites having been launched, the wire is veered out against the foot brake or hauled in by the engine working in reverse gear. The car is prevented from riding off the jack when hauling in, by putting on the hand brake which has been disconnected from the off-side wheel. Care must be taken to avoid putting too great a strain on the wire when hauling in. When the net is being sent to heights over 1500 ft., another lifting kite is attached to the wire so that as much wire again may be carried into the air.

Warning banners, according to Air Ministry regulations, are attached to the wire every 300 ft. to show the position of the wire to passing aircraft pilots.

The collecting net

The net resembles the marine tow-net and is made in three sections: first, a cylinder of very wide mesh netting 20 in. long fastened to a wooden hoop 1 yd. in diameter; secondly, a conical bag of muslin 1 yd. in diameter in front and 3 yd. long tapering to join the third section, which is a small calico

cylinder just big enough to surround a strong glass specimen tube to hold the insects caught. Three whipcord bridles are attached to the hoop. At the junction of the wide mesh netting and the muslin bag is a band of tape round the net, and to the outside of this are sewn at equal intervals twelve small rings. Two separate cords, each arranged as a freely running noose, pass through these rings; one keeps the net closed on ascent until released by the mechanism about to be described, and the other closes the net again for descent after the bridles have been released, also by the action of the mechanism.

The opening and closing mechanism

Originally it was intended to use a clockwork mechanism, and later Mr Freeman constructed such a device, but for the greater part of the time a

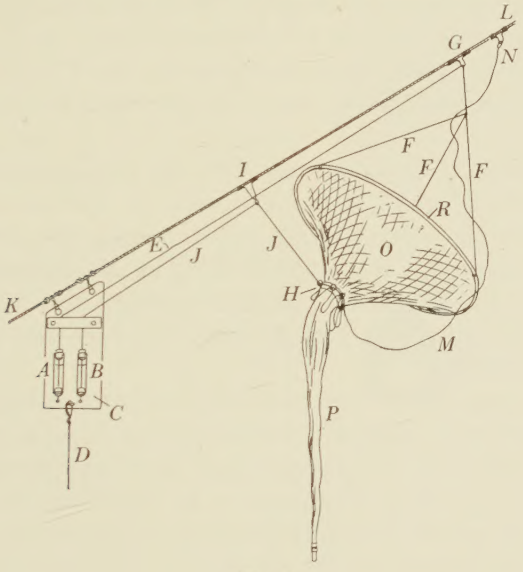

Fig. 1.

very simple, efficient and light chemically controlled mechanism was used and found very satisfactory. It works by the action of nitric acid on copper wire.

The letters in the following description refer to those in Fig. 1; the mechanism is also seen in Pl. 8, phots. 1 and 2. *A* and *B* are two small glass tubes, corked at each end, attached to a plywood board *C* which hangs by brass wires from the kite line *KL*. Each tube has a copper wire passing through it. That passing through the tube *A* is fixed below the tube to the board *C* and fastened above the tube to a cord *E*; this, leading through a guide on the board, is fastened at its other end to the bridles *F* of the net, after having passed through the wire loop *G* which suspends the net from the kite line *KL*. The net is kept closed on ascent by a cord *J* drawn tight through the small rings sewn on the tape round the net at *H*; this cord passes back, through the wire loop *I* on the

kite line, to be fastened to the upper end of the copper wire which passes through the tube *B*. Another cord *M*, also forming a noose through the rings *H*, but left quite slack, is fastened to the kite line at *N*.

The tube *A* is filled with weak acid and the tube *B* with stronger acid, and the apparatus is ready for ascent. On going up the collecting net proper *P* is kept closed by the cord *J* drawn tight through the rings *H*; the part *O* connecting the net proper to the ring *R* is a cylinder of wide open mesh netting which will allow any insects to pass through. Soon after the net has reached the desired height the copper wire in tube *B* is eaten through by the stronger acid so that the cord *J* is released and the muslin collecting net *P* flies open in the wind with the bridles pulling on the cord *E*.

The weaker acid in tube *A* is made up to such a strength that it will eat through its copper wire in approximately 1 hr., 2 hr. or such time as is desired. At the end of this period the cord *E* is released and the net falls to be caught by the cord *M* which tightly throttles the muslin net *P* and so prevents any further capture of insects. The apparatus is now ready for hauling down (see Pl. 9, phot. 5).

The speed of the acid reaction varies with the temperature, but by using a thermometer as a rough guide to the conditions the operator can after a little experience time the exposure to within a few minutes. The actual duration of the exposure is observed and recorded. With an air temperature near the ground of 20° C. and acids of 50 and 25% strength the net will open in a quarter of an hour, and remain open for 2 hr. The wire used in the fuses was 24 S.W.G. tinned copper.

Lateral movements of the kites tend to swing the fuse board from side to side and may eventually cause it to turn completely round the kite line and entangle the control cords. To prevent this a small lead weight is hung from the lower edge of the board at *D* by about 12 ft. of cord, and its oscillations are damped out by the addition of a baffle consisting of two pieces of plywood interlocking at right angles (see Pl. 8, phot. 1). The lead weight and baffle swing gently to and fro at the end of the cord and ensure the smooth working of the mechanism under all normal working conditions.

The simplicity and reliability of the method and its ability to withstand the severe buffeting of the wind and weather are compensation for the more precise timing which would be given by a clockwork or electrical device.

4. Method of kite flying

In light winds the pilot kite is started by throwing it into the air at the end of the full length of inter-kite rope (350 ft.), and simultaneously hauling in with the engine, so that the kite rapidly soars to a level where the wind is sufficiently strong to maintain it. The rope is now veered out slowly to the point where it is connected to the main length of piano-wire. Here the second kite is inserted along with the short piece of strong rope supporting the net and

Phot. 4.

Phot. 5.

Phot. 4. Net opened for collecting.
Phot. 5. Net closed prior to hauling down.

fuse board. When these are correctly adjusted with the net in the closed position ready for ascent the fuse tubes are filled with acid of appropriate strengths by a pipette. (A series of 30 c.c. vials is kept at hand, storing small quantities of nitric acid in strengths varying from 20 to 50%.) The whole system is then veered out as quickly as conditions permit, attaching the red and white warning banners every 300 ft., until the desired height is reached. After the drum is stopped the kites continue to rise for a short period before settling down to a steady angle of flight. After a few minutes the first fuse breaks and the net flies open into the collecting position. (Pl. 9, phot. 4.)

In moderate to fresh winds the pilot kite may be launched at a short distance and the rope veered out immediately without any preliminary hauling in.

During flight the kite is from time to time observed through a small telescope mounted on a quadrant on a levelled tripod so that its height may be calculated from a measurement of the angle of the telescope and a knowledge of the length of wire out, an allowance being made for the catenary curve of the line. The amount of line out is recorded by an adaptation of a cyclometer.

After the closing of the net the wire is hauled in under engine power and the net detached from the kite line as soon as it reaches the ground. The whole of the muslin part of the net, together with the glass tube, is put into a large cyanide killing jar. After death those insects still clinging to the inside of the net are shaken down to join those already in the tube. The inside of the net is searched and any insects which are found *dead* added to the tube; any living insects found are not included, since these might have alighted on the net in the course of examination.

Before the ascent the net is scrutinized to see that no insects have crawled or flown into it before it is closed, and as already explained the wide-mesh netting in front of the closed muslin net allows any insects encountered during ascent to pass through uncaught.

5. Description of experiments 1932–5

The experiments were made during the summer months of the years 1932–5. The particulars of date, position, time and duration of net exposure, height and meteorological conditions and total catch of insects at each station are given in Table 1. The details of the nature of the catch are given in § 6.

The majority of the flights were made at Hull from the playing fields of the University College lying on the N.W. outskirts of the city, where a good exposure to winds in all directions is available. One of the objects of our investigations is to study the infection of this country by small wind-borne insects from abroad, as distinct from the larger true migrants being investigated by others. For this purpose we took the apparatus to the coast of Suffolk at Thorpeness in July 1933, and to the top of the 500 ft. Abbot's Cliff between Folkestone and Dover in July and August of the same year and in

Table 1. *Station list, meteorological observations and records of total catch*

Station number	Date	Position	Time of exposure (G.M.T.)	Duration of exposure (hr.)	Height of net (ft.)	Wind direction, force of wind and state of weather*		Atmospheric pressure in millibars	Temp. ° F.	Relative humidity %	Total catch
	1932										
1	18 May	Hull	1530–1645	1¼	150–200	S. by W.	3 c	1021·0	68	55	48
2	19 ,,	,,	1225–1355	1½	150–200	S.S.W.	2 c	1019·4	66	59	31
3	19 ,,	,,	1510–1640	1½	250	S.S.W.	2 c	1018·0	66	59	9
4	19 ,,	,,	1705–1805	1	250–300	S.S.W.	2 c	1017·5	66	59	12
5	2 June	,,	1230–1430	2	200–300	N. by E.	4–5 bc	1018·0	58	64	23
6	2 ,,	,,	1730–1930	2	250–350	N.N.E.	4–3 bc	1018·1	53	68	8
7	7 ,,	,,	1730–1830	1	250–350	W.	3 c	1025·7	58	64	10
8	18 ,,	,,	1730–1900	1½	150–250	N.N.E.	3–4 bcc	1024·5	55	69	3
9	24 ,,	,,	1515–1615	1	200–300	W.	4 c	1022·0	67	55	9
10	29 ,,	,,	1500–1630	1½	200–250	S.S.E.	3 b	1016·5	66	70	5
11	18 July	,,	1230–1430	2	250–350	N.	5 c	1021·0	57	82	2
12	5 Aug.	Aldbrough, E. Yorks	1500–1630	1½	250–300	N.W. by W.	3 c	1022·5	66	65	13
13	15 ,,	Hull	1420–1620	2	250–300	E.	4 c	1023·3	66	60	18
14	17 ,,	,,	1050–1250	2	250–350	W.	3–4 b	1025·0	77	50	7
15	17 ,,	,,	1320–1450	1½	200–350	W.	4 b	1025·0	77	50	14
16	5 Sept.	,,	1350–1550	2	300–350	W.	3–4 c	1014·0	64	73	5
17	6 ,,	,,	1520–1650	1½	300–350	W.	3 bc	1006·5	62	70	4
18	12 ,,	,,	1500–1700	2	350–400	W.	4 bcc	1016·5	61	48	11
19	26 ,,	,,	1240–1420	1½	275–325	W.	3 b, bc, c	1006·0	59	71	3
20	27 ,,	,,	1350–1650	3	300–350	N.	3 bc	1026·0	52	50	9
21	29 ,,	,,	1230–1430	2	300–350	N.E. by E.	4 bc	1024·4	61	67	33
22	29 ,,	,,	1440–1640	2	300–350	N.E. by E.	4 bc	1020·0	58	68	6
23	6 Oct.	,,	1145–1345	2	325–375	S.E. by S.	3 bz	1016·0	58	53	15
24	31 ,,	,,	1355–1555	2	350–375	N.N.E.	4 b	1016·0	45	60	6
	1933										
25	26 April	,,	1450–1530	¾	250–350	S.	3-4 c	1014·2	56	65	1
26	19 May	,,	1430–1600	1½	200–450	S.	2–3 bcz	1022·0	66	55	8
27	29 ,,	,,	1535–1605	½	350–450	N.E. by E.	3–5 bcc, bc	1023·5	54	65	2
28	31 ,,	,,	1545–1645	1	250–350	S. by E.	5 b	1017·6	64	50	18
29	1 June	,,	1430–1555	1½	720–850	S.E.	5–6 bcz	1021·0	64	55	2
30	2 ,,	,,	1440–1540	1	450–500	S.	4–5 bcc, o	1021·0	70	50	16
31	7 ,,	,,	1510–1610	1	200–300	S.E.	3–5 b	1020·0	75	40	9
32	8 ,,	,,	1420–1650	1½	200–500	N.E.	4–5 b, bc, m	1025·0	65	70	14
33	13 ,,	,,	1310–1540	1½	500–600	N.E.	5–6 o, d	1016·5	54	74	0
34	28 ,,	,,	1500–1600	1	300	N.	3–4 bcc	1014·2	65	60	8
35	16 July	,,	1430–1730	3	300–350	N.	6 b	1014·0	65	80	5
36	26 ,,	Thorpeness	1310–1510	2	380–630	S.S.W.	5 b	1017·2	77	65	41
37	26 ,,	,,	1545–1745	2	410–610	S.W.	5 b	1017·0	74	65	34
38	28 ,,	,,	1040–1140	1	150–410	W.	2–5 b	1019·0	70	45	18

39	28 „	„	1330–1430	1	280–480	S.W.	4–5	bbc	1019·2	73	45	15
40	2 Aug.	Abbot's Cliff	1637–1737	1	480	S.W.	6	bcz	1028·0	75	50	8
41	4 „	„	1705–1805	1	150	N.E.	3	bc	1024·7	73	55	7
42	5 „	„	1110–1210	1	350	E.	4–5	b	1024·0	72	55	3
43	5 „	„	1525–1610	$\frac{3}{4}$	450	N.E.	6	b	1023·0	73	70	23
44	8 „	„	1324–1625	3	450	S.W.	4	b, bc, c	1016·4	77	60	39
45	9 „	„	1740–1900	$1\frac{1}{4}$	250–350	S.W.	4	bc	1018·0	68	75	4
46	10 „	„	1320–1350	$\frac{1}{2}$	600	N.W.	5	c	1021·6	76	45	6
47	13 „	„	1150–1420	$2\frac{1}{2}$	350–600	E.	3–4	bc	1023·6	68	45	18
48	13 „	„	1445–1650	2	450–600	E.	6–8	bc, c	1022·0	68	50	14
49	4 Sept.	Hull	1515–1700	$1\frac{1}{4}$	500–1200	N.W. by W.	3–5	bc	1026·3	70	60	6
	1934											
50	2 May	„	1445–1625	$1\frac{1}{2}$	275–375	E.N.E.	3–4	bc	1013·6	60	60	1
51	3 „	„	1440–1620	$1\frac{1}{2}$	450–550	E.N.E.	3	b	1015·5	52	82	0
52	1 June	„	1355–1510	$1\frac{1}{4}$	250–350	N.N.E.	3	b	1022·1	64	50	17
53	4 „	„	1430–1500	$\frac{1}{2}$	400–450	N.E. by N.	4–5	c, bbc	1020·5	57	84	0
54	11 „	„	1420–1540	$1\frac{1}{2}$	500–600	N.E.	3–5	b	1019·3	65	70	4
55	27 „	„	1430–1535	1	500–550	W.	3–4	o, bcc	1013·5	70	55	1
56	27 „	„	1610–1640	$\frac{1}{2}$	500–550	W.	3–4	o, bcc	1013·2	65	55	5
57	29 „	„	1500–1610	$1\frac{1}{4}$	500–550	N.E. by E.	3	o, bc, b	1025·0	60	55	5
58	19 July	„	1055–1310	$2\frac{1}{4}$	400–450	N.W. by W.	5–6	bc	1012·0	70	62	14
59	20 „	„	1440–1540	1	450–500	S.E.	3–4	bcc	1010·0	68	60	13
60	23 „	E. Yorks wolds	1500–1600	1	1600–2100	N.W. by W.	3–4	bc	1013·3	72	70	18
61	30 „	Abbot's Cliff	1530–1645	$1\frac{1}{4}$	200–750	S.W.	4–2	bcz	1011·5	70	70	0
62	31 „	„	1555–1755	2	600–650	W.S.W.	4–5	c, bc	1008·6	68	75	1
63	1 Aug.	„	1435–1735	3	450–500	S.W. by W.	4	bcc	1012·1	66	75	0
64	3 „	„	1240–1520	$2\frac{1}{2}$	850–900	S.W.	4	c, bc	1007·0	67	65	0
65	9 „	„	1315–1515	2	800–900	W.	3–4	bc	1013·0	61	90	13
66	9 „	„	1545–1645	1	800–900	W.	3–4	bc	1010·0	60	90	8
67	3 Sept.	Hull	1515–1615	1	800–850	S.W.	4–5	bc	1008·2	65	65	7
68	9 „	„	1640–1755	$1\frac{1}{4}$	650	S.W. by W.	3–4	bc	1010·0	60	78	6
69	10 „	„	1615–1715	1	600–800	S.W.	3–4	b	1020·0	65	85	32
70	18 „	„	1525–1625	1	600–650	S.W.	3–4	bcc	1013·9	65	75	7
71	25 „	„	1515–1645	$1\frac{1}{2}$	550–900	S.W. by W.	3–4	b	1015·0	58	78	11
	1935											
72	9 May	„	1645–1800	$1\frac{1}{4}$	1650–2240	?	?	b, bc	1006·0	54·5	60	0
73	29 „	„	1600–1700	1	1300–1700	E.N.E.	3–4	?	1001·0	57·0	60	2
74	25 Aug.	„	1135–1235	1	400–1000	E.	3–4	b	1026·0	82	70	1
75	25 „	„	1510–1725	$2\frac{1}{4}$	950–1500	E.S.E.	3–4	bc	1008·0	86	66	4
76*a*	27 „	„	1435–1705	$2\frac{1}{2}$	850–1250	W.N.W.	3–4	bc	1004·0	67	58	20
b	27 „	„	1600–1630	$\frac{1}{2}$	180–370	W.N.W.	3–4	bc	1004·0	67	58	10
77*a*	30 „	Tetney	1350–1620	$2\frac{1}{2}$	400–1400	S.S.W.	6	cr	1005·0	67	60	4
b	30 „	„	1410–1620	$2\frac{1}{4}$	350–800	S.S.W.	6	cr	1005·0	67	60	1
78	1 Sept.	Hull	1600–1730	$1\frac{1}{2}$	450–2350	S.	4–5	bccR	1006·0	74	76	1
79	26 „	Cave wold	1645–1815	$1\frac{1}{2}$	550–2000	?	5	?	1008·0	78	74	10
80	2 Oct.	„	1540–1715	$1\frac{1}{2}$	1550–1750	S.	4–5	?	958·0	53	71	0

* In the Beaufort weather notation.

August 1934. During our visits to the Suffolk and Kent coast we received valuable assistance in the field from Mr R. Liddington. The coast at Thorpeness is low-lying with a shingle beach from which the flights were made, with a hinterland of undulating wold country. Whilst good collections were made at these points, the winds on each occasion for the whole period of our visits were towards instead of from the sea. That aerial currents must be important agents in carrying small insects to this country was, however, demonstrated by the collections made in the summer of 1936 (Hardy & Milne, 1937) when nets were flown from kites and from the mast-head on the Ministry of Agriculture and

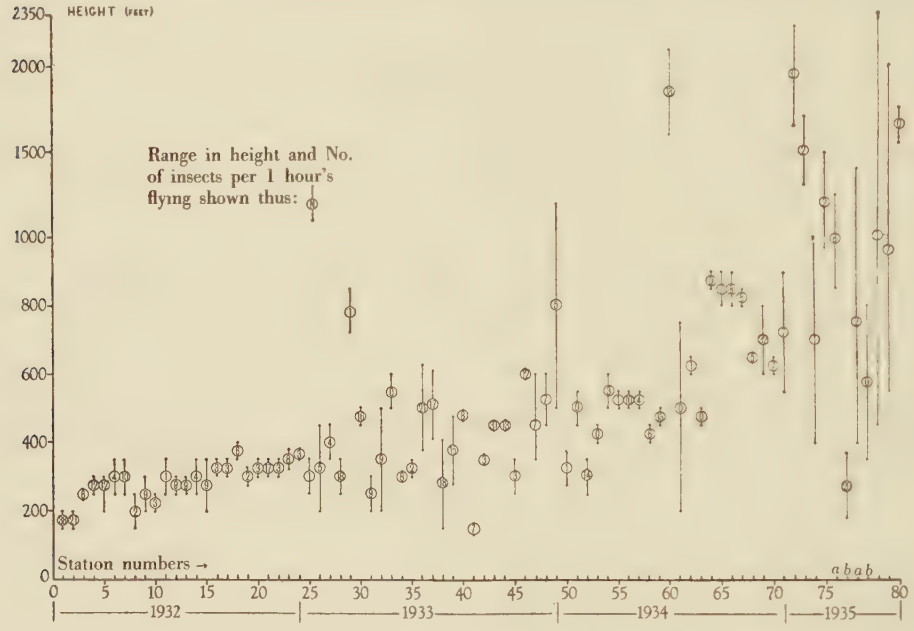

Fig. 2. Chart showing the ranges of height sampled in the series of experiments during the summers of 1932–5 together with the number of insects caught per 1 hr. collecting in each net. The nets were of uniform pattern, 3 ft. diameter opening, and kept closed on the way up and down.

Fisheries research ship *George Bligh* during one of her routine cruises over the North Sea. Numbers of insects were taken at distances between 100 and 150 miles from land. The collections made on the Suffolk and Kent coasts show how vast a population of insects is constantly being swept out to sea.

Other flights were made on the east Yorkshire wolds near Market Weighton and at Cave Wold, at Tetney near Grimsby, and at Aldbrough on the east Yorkshire coast.

The flights in 1932 were made with a simpler technique than that described above. A smaller pilot kite, a rope line and a hand winch were used; the net being opened and closed by pulling a light cord looped up at intervals

to the main line. The weight and wind resistance of the rope line and the smaller lifting power of the pilot kite limited the flights to 450 ft. The automatic net control and power winch were introduced at the beginning of the 1933 season, and the heights reached were gradually increased to over 2000 ft. In 1935 Mr Freeman introduced a clockwise release mechanism to control the opening and closing of the net.

Fig. 2 shows graphically the ranges in height sampled by the nets in the whole series of the experiments. The numbers in the circles represent the numbers of insects taken per 1 hr. collecting during each flight. It is seen that as we extended the height of sampling, it became more difficult to keep the kites at an even level, and a considerable range of varying height was usually experienced in the higher flights. Whilst the greatest height reached was 2350 ft., the highest steady flight was for a period of 1 hr. 25 min. at 1550–1750 ft.

Altogether 82 samples were taken yielding a collection of 839 insects during a total flying time of 124·5 hr.

6. Nature of the aerial plankton

With the exception of the single specimen of the butterfly *Pieris rapae*, all the insects taken belong to families of small- or light-bodied insects with rather weak powers of flight, but with relatively large wing surfaces compared with body mass (see Pl. 10, phots. 6 and 7). They may truly be described as drifting in the aerial currents and so may justly be described as aerial plankton. The Aphididae, of which 250 individuals were taken in our collections, forming 30% of the total insect catch, are particularly well adapted to transit by aerial currents.

Table 2 gives the catches at each station analysed into families, the stations being arranged in order of height (the mean height for each flight) from the highest at the top of the table to the lowest at the foot. This table thus represents a section of the aerial plankton as sampled in our experiments between 150 and 2000 ft. The number of occasions on which each family occurred, together with the total number of individuals of each family, are given at the foot of the table.

The Aphididae, Acalypterae, Mycetophilidae and Chalcidoidea (in order of numerical importance) together form 69·5% of the total collections.

A list of all species identified is given in Table 10 at the end of the paper, together with the stations at which they occurred. Many of those taken in 1935 were not determined beyond the family.

A more general impression of the composition of the aerial plankton may be obtained from Table 3 and Fig. 3, wherein are shown the numbers of the representatives of the more important families taken per 10 hr. collecting at different height ranges up to 2000 ft.

Table 2. *Analysis of samples into families. The samples are arranged in descending order of height. The mean height of each net is given and the range of height may be found on reference to Table* 1

Height of net (ft.)	Station No.	Hemiptera: Psyllidae	Hemiptera: Jassidae	Hemiptera: Aphididae	Hemiptera: Thysanoptera	Coleoptera: Staphylinidae	Coleoptera: Chrysomelidae	Diptera: Muscetophilidae	Diptera: Cecidomyiidae	Diptera: Chironomidae	Diptera: Agromyzidae	Diptera: Chloropidae	Diptera: Ephydridae	Diptera: Sphaeroceridae	Diptera: Other Acalypterae	Hymenoptera: Ichneumonoidea	Hymenoptera: Chalcidoidea	Hymenoptera: Proctotrypoidea	Other insects	Total catch
1945	72	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
1825	60	.	.	11	1	.	.	.	.	.	.	1	1	.	.	1	3	.	—	18
1650	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
1500	73	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	—	2
1400	78	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	—	1
1275	79	.	1	6	.	.	.	2	.	1	.	.	.	.	.	.	.	.	—	10
1225	75	.	1	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.	—	4
1050	76*a*		.	.	.	.	12	.	.	.	.	2	1	.	.	1	.	3	(Arachnida: Araneida 1)	20
900	77*a*	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	1	—	4
875	64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
850	49	1	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	1	Psocoptera 1	6
850	65	.	.	1	1	.	.	.	.	1	.	4	.	.	.	1	5	.	—	13
850	66	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	7	.	—	8
825	67	.	.	6	.	.	.	.	.	.	.	.	.	.	.	1	.	.	—	7
725	71	4	.	2	.	.	.	.	.	.	.	.	.	.	.	3	.	.	Diptera, Bibionidae 2	11
700	69	3	.	22	.	1	.	1	.	.	.	.	.	.	1	.	1	.	Psocoptera 3	32
700	74	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	—	1
675	29	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	—	2
650	68	.	.	1	.	1	.	.	.	.	.	.	.	.	.	2	1	.	Psocoptera 1	6
625	62	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	—	1
625	70	.	.	5	.	.	.	.	.	.	.	.	.	.	.	2	.	.	—	7
600	46	.	.	.	1	.	.	.	.	.	.	3	.	.	.	.	2	.	—	6
575	77*b*	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	1
550	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
550	54	.	1	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	—	4
525	48	.	2	1	.	.	.	.	.	.	1	4	.	.	1	.	1	.	Hemiptera: Delphacidae 1 Lygaeidae 1 Diptera: Empididae 1 Phoridae 1	14
525	55	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	1
525	56	.	2	.	.	.	.	.	1	.	.	.	1	.	.	1	.	.	—	5
525	57	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	—	5

500	36	1	.	10	5	.	.	.	.	.	.	.	2	.	.	10	5	3	Hymenoptera, Cynipoidea 5	41
500	37	.	1	9	.	.	.	.	.	.	.	.	1	.	.	4	1	2	Hymenoptera: Cynipoidea 5 Undetermined 11	34
500	51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
475	30	.	.	12	2	.	.	.	.	.	.	.	.	1	.	.	.	.	Hemiptera, Delphacidae 1	16
475	40	.	.	1	.	.	.	.	.	.	.	1	.	.	.	3	1	1	Diptera, Drosophilidae 1	8
475	47	.	1	2	.	.	.	.	.	.	.	11	.	.	.	.	3	.	Coleoptera, undetermined 1	18
475	59	.	1	3	2	2	.	.	.	.	.	.	.	.	1	.	3	.	Lepidoptera, Pieridae 1	13
475	61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
475	63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
450	43	.	1	3	.	.	1	.	.	.	.	.	.	.	.	.	12	2	Hemiptera, Delphacidae 1 Hymenoptera, Cynipoidea 1 Diptera: Lonchopteridae 1 Drosophilidae 1	23
450	44	1	.	15	2	.	.	1	.	.	1	4	.	1	.	2	9	.	Neuroptera, Coniopterygidae 1 Hemiptera, Delphacidae 1 Coleoptera, undetermined 1	39
425	53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	Nil
425	58	.	.	8	3	.	.	.	.	.	.	.	.	.	2	.	1	.	—	14
400	27	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	—	2
375	18	.	.	4	.	.	.	2	.	.	.	2	.	.	1	2	.	.	—	11
375	24	.	.	1	.	2	.	1	.	.	.	.	.	1	.	.	.	.	Diptera, Tipulidae 1	6
375	39	.	1	4	1	.	.	3	.	.	.	.	.	.	.	2	4	.	—	15
350	23	4	1	7	.	.	.	.	.	.	.	.	.	2	.	.	1	.	—	15
350	32	.	.	9	.	.	.	1	1	.	1	.	.	.	1	.	.	.	Diptera, undetermined 1	14
350	42	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	—	3
325	16	.	1	1	.	.	.	1	.	.	.	.	2	.	.	.	.	.	—	5
325	17	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	—	4
325	20	.	.	2	.	.	.	2	.	.	.	1	2	.	.	.	.	.	Diptera: Empididae 1 Drosophilidae 1	9
325	21	.	.	3	.	3	.	4	.	.	.	1	1	6	2	.	5	.	Diptera: Phoridae 7 Drosophilidae 1	33
325	22	.	.	3	.	.	.	.	.	.	.	.	.	1	.	.	2	.	—	6
325	26	.	.	1	.	3	.	.	2	.	.	.	.	.	1	.	.	.	Diptera, Bibionidae 1	8
325	35	1	1	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	—	5
325	50	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	—	1
300	6	.	.	2	.	1	.	3	.	.	.	.	.	.	.	.	.	.	Diptera: Psychodidae 1 Undetermined 1	8
300	7	.	.	1	.	.	.	.	.	.	.	.	.	.	8	.	.	.	Hymenoptera, undetermined 1	10
300	11	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	Diptera, Cordyluridae 1	2
300	14	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	2	.	—	7
300	19	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	3
300	25	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	—	1
300	28	.	.	14	.	.	.	2	.	.	.	.	.	.	1	1	.	.	—	18
300	34	.	.	3	.	.	.	.	1	.	.	.	2	.	.	1	1	.	—	8

Table 2 (*cont.*)

Height of net (ft.)	Station No.	Hemiptera			Thysanoptera	Coleoptera		Diptera								Hymenoptera			Other insects	Total catch
		Psyllidae	Jassidae	Aphididae		Staphylinidae	Chrysomelidae	Mycetophilidae	Cecidomyidae	Chironomidae	Agromyzidae	Chloropidae	Ephydridae	Sphaeroceridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Proctotrypoidea		
300	45	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	— —	4
300	52	.	.	1	2	2	.	4	1	1	.	2	.	.	1	1	1	.	Diptera, Empididae 1	17
275	4	.	.	1	.	1	.	5	.	1	.	.	.	.	3	.	.	.	Coleoptera, Hydrophilidae 1	12
275	12	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	1	.	Diptera, Cordyluridae 1 Hymenoptera: Cynipoidea 2 Undetermined 1	13
275	13	1	.	5	.	1	.	8	.	.	.	1	.	1	.	.	1	.	— —	18
275	15	.	.	9	.	.	.	.	.	.	.	2	.	.	.	1	1	1	— —	14
275	38	.	.	4	.	.	.	.	.	.	.	.	.	1	9	.	.	1	Hymenoptera, undetermined 3	18
275	76*b*	.	.	.	.	.	8	.	.	.	.	.	1	.	.	.	1	.	— —	10
250	3	.	.	1	.	3	.	5	.	.	.	.	.	.	.	.	.	.	— —	9
250	5	.	.	.	.	.	.	8	.	.	.	.	6	.	3	.	.	.	Hemiptera, Delphacidae 1 Hymenoptera, undetermined 5	23
250	9	.	1	3	.	.	.	.	.	.	.	.	2	.	.	3	.	.	— —	9
250	31	.	.	5	.	1	.	2	.	.	1	.	.	.	.	.	.	.	— —	9
225	10	.	.	2	.	.	.	.	.	1	1	1	.	.	.	.	.	.	— —	5
200	8	.	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	— —	3
175	1	.	.	17	.	1	.	19	.	.	.	.	.	.	7	.	.	.	Diptera: Rhyphidae 1 Lonchopteridae 1 Muscidae 1 Undetermined 1	48
175	2	.	.	4	.	2	.	15	.	.	.	.	.	.	6	1	.	.	Diptera: Empididae 1 Hymenoptera, undetermined 2	31
150	41	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	Diptera: Drosophilidae 1 Sepsidae 1 Hymenoptera, Cynipoidea 1	7
Totals:																			— —	
No. of occurrences		8	23	55	10	18	6	23	6	7	7	19	14	8	18	21	30	9	86 (including 1 spider)	839
No. of individuals		16	28	250	20	30	24	92	7	7	7	45	24	14	50	45	79	15		

Phot. 6. Sample of aerial plankton taken in a 3 ft. diam. net during an hour's collecting at 1600–2100 ft. at Station 60 (see Table 1).

Phot. 7. Sample of aerial plankton taken in a 3 ft. diam. net during an hour's collecting at 600–800 ft. at Station 69 (see Table 1). Magnification as in phot. 6.

Table 3. *Number of insects per 10 hr. collecting at different height ranges*

Height in ft.	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Other insects	Total
1000–2000	2·4	14·4	0·0	11·2	1·6	4·0	1·6	0·0	1·6	2·4	4·8	44·0
750–1000	1·0	8·0	0·0	1·0	1·0	4·0	0·0	0·0	2·0	13·0	8·0	38·0
500–750	5·0	16·5	2·0	0·0	1·0	4·5	0·5	2·0	4·0	2·5	10·5	48·5
250–500	1·8	22·3	2·3	1·3	5·4	3·7	1·7	7·9	4·1	8·3	17·4	76·2
150–250	0·8	28·6	8·2	0·0	40·0	0·8	7·3	16·3	3·3	0·0	11·6	116·9
Total	11·0	89·8	12·5	13·5	49·0	17·0	11·1	26·2	15·0	26·2	52·3	323·6

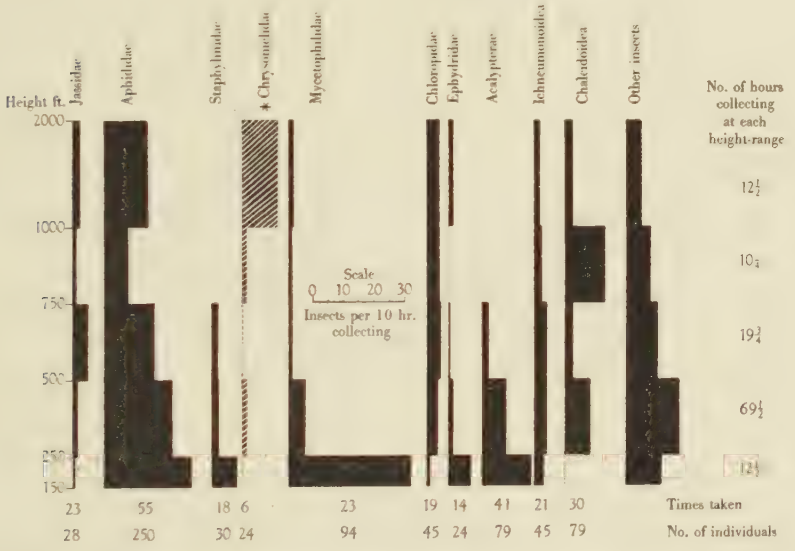

Fig. 3. Graphic representation of the composition of the aerial plankton between 150 and 2000 ft. The blocks represent the average number of insects of different families taken in each height range per 10 hr. collecting (from Table 3). The numbers of individuals and the number of occurrences on which they are based are given below the figure. The chrysomelid figures are largely influenced by observations at one station (see text).

In Table 4 the vertical distribution of each of these same families is shown by expressing the average numbers of any one family per 10 hr. collecting at each height range, as a percentage of the total of that family taken (per 10 hr. collecting) at all height ranges. The results are shown graphically in Fig. 4, where the families are rearranged in a series passing from those with lower to those with higher vertical distributions. The total numbers of insects of each family on which the calculations are based are shown below the name of the family. The apparent irregularity in vertical distribution in some families is no doubt due to the paucity of the data available; nevertheless, we obtain a

good general indication of the relative heights usually reached by the different families.

Table 4. *Percentage distribution over ranges of height for each of the more important families* (*each column totalling* 100 *vertically*)

Height in ft.	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Other insects	All insects
1000–2000	21·8	16·0	0·0	83·0	3·3	23·5	14·4	0·0	10·7	9·2	9·2	13·6
750–1000	9·1	8·9	0·0	7·4	2·0	23·5	0·0	0·0	13·3	49·6	15·3	11·7
500–750	45·4	18·4	16·0	0·0	2·0	26·5	4·5	7·6	26·7	9·5	20·1	15·0
250–500	16·4	24·8	18·4	9·6	11·0	21·8	15·3	30·2	27·3	31·7	33·3	23·5
150–250	7·3	31·9	65·6	0·0	81·7	4·7	65·8	62·2	22·0	0·0	22·1	36·2

Fig. 4. Chart showing the percentage distribution of the more important families at different height ranges arranged from left to right in ascending order of height distribution (see Table 4).

The comparative uniformity in distribution of the Aphididae, Ichneumonoidea and Chloropidae up to 2000 ft. is well brought out. The surprising distribution of the Chrysomelidae is omitted from Fig. 4: it must be taken with reserve, since it is based on only six occurrences and 24 individuals of which 20 were taken on the same day (27 August 1935).

In Table 5 the numbers of the representatives of these same families are shown as *percentages of the total catch* of all insects per 10 hr. collecting *at each height range*. From this we may see the relative percentage composition of the aerial plankton within each height range. Above 100 ft. the Aphididae, Chrysomelidae (see qualification above), Chloropidae and Chalcidoidea are the more important elements. Estimates of the density of the aerial drifting insect populations are given in § 8.

A comparison may be made here between the results of our experiments and those made by collecting from aeroplanes by Collins & Baker (1934) in America, and by Berland (1935) in France. Coad, who made aeroplane

Table 5. *Percentage composition of the aerial plankton within each height range (each line totalling 100 horizontally)*

Height in ft.	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Other insects
1000–2000	5·5	32·7	0·0	25·5	3·6	9·0	3·6	0·0	3·6	5·5	11·0
750–1000	2·4	21·1	0·0	2·6	2·6	10·5	0·0	0·0	5·2	34·2	21·4
500–750	10·3	34·0	4·1	0·0	2·1	9·3	1·0	4·1	8·2	5·1	21·8
250–500	2·4	29·3	3·0	1·7	7·1	4·9	2·2	10·4	5·4	10·9	22·7
150–250	0·7	24·4	7·0	0·0	34·2	0·7	6·2	13·9	2·8	0·0	10·1

collections in America (1931), gives no details of his catches[1]. Collins & Baker, using opening and closing screens, in May 1932 caught 25 insects during 9 flights between 300 and 5000 ft., and in May 1933, caught 28 insects during 14 flights between 500 and 3000 ft. Berland in 1934, using nets instead of screens, caught 38 insects during 12 flights (June to September) at heights varying from 1500 to 7000 ft. The following is a list of the families recorded by them; the letters "C & B" and "B" indicate whether they were taken by Collins & Baker or by Berland, and the letter "K" is also added against those families which were taken in our kite-net experiments.

COLLEMBOLA	Sminthuridae	B	—	—
THYSANOPTERA	—	B	—	K
PSOCOPTERA	—	B	—	K
HEMIPTERA	Capsidae	—	C & B	—
	Jassidae	B	—	K
	Psyllidae	B	C & B	K
	Aphididae	B	—	K
COLEOPTERA	Carabidae	—	C & B	—
	Staphylinidae	—	C & B	K
	Byrrhidae	—	C & B	—
	Helodidae	—	C & B	—
	Chrysomelidae	B	—	K
LEPIDOPTERA	Lymantriidae (Gipsy moth larvae)	—	C & B	—
DIPTERA	Tipulidae	—	C & B	K
	Chironomidae	—	C & B	K
	Cecidomyidae	B	C & B	K
	Mycetophilidae	—	C & B	K
	Bibionidae	—	C & B	K
	Empididae	—	C & B	K
	Lonchopteridae	—	C & B	K
	Phoridae	—	C & B	K
	Ephydridae	B	C & B	K
	Chloropidae	B	C & B	K
	Sphaeroceridae	—	C & B	K
	Heleidae	B	—	—
	Cypselidae	B	—	—
HYMENOPTERA	Braconidae	B	C & B	K
	Chalcididae	B	C & B	K
	Proctotrypidae	—	C & B	K
ARACHNIDA	—	—	C & B	K

Particularly interesting are the specimens of gipsy moth larvae (*Lymantria dispar*) taken by Collins & Baker (one specimen at 2000 ft.) and the collembolan *Bourletiella lutea* by Berland between 3250 and 4000 ft.

[1] See Addendum note on p. 226.

The following is a list of those species or related species which are common to two or all three collections together with the heights at which they were taken; the letters C & B, B, and K indicate the collections as before.

Psyllidae: *Aphalara* sp. C & B, 2000; *A. calthae* Linn. K, 500.

Jassidae: *Deltocephalus pascuellus* Fall. B, 3900; K, 350.

Chloropidae: *Oscinis* (*Oscinella*) *frit* Linn. C & B, 2000; K, 600.

Lonchopteridae: *Lonchoptera lutea* Fall. C & B, 500; K, 450.

Ephydridae: *Hydrellia flaviceps* Mg. B, 3250; *H. griseola* Fall. B, 4900; *H. incana* Stenh. K, 300.

Braconidae: *Aphidius nigripes*, C & B, 1500; *Aphidius* sp. K, 480.

Chalcididae: *Cyrtogaster vulgaris* Walk. C & B, 2300; K, 410.

The results of all three collections emphasize the fact that the aerial plankton is essentially made up of weak flyers of small size with a large surface-weight ratio. In the case of our kite-net experiments the method of collecting by means of a net suspended passively in the air is definite evidence that the insects at the time of their capture were being carried along by the prevailing air currents and that they were not engaged in making independent directional flights. In order to test whether strong-flying insects might be caught, but subsequently escape from our nets, such insects as bluebottles, wasps and bees were on several occasions placed (uninjured and in good condition) in the net before the ascent; in every case the insects were found to be still in the net at the end of the exposure along with the catch proper.

7. Influence of weather conditions

There can be no doubt that marked differences in weather conditions must have an important effect on the numbers of insects being carried in the aerial currents. In a flight made at Hull on 13 June 1933 (Station 33), in an easterly wind of 20–25 m.p.h., the net was flying between 500 and 600 ft. just under the cloud base (at times just within it), where the air was saturated with moisture; the catch for 1·5 hr. collecting was nil. This may be contrasted with the four flights made at Thorpeness on 26 and 28 July of the same year (Stations 36–39), when the wind was westerly and rather variable, averaging some 15 m.p.h., and the weather was hot and sunny towards the end of a period of anticyclonic conditions. Here the catches were 21, 17, 18 and 15 insects per hour's collecting.

Altogether 82 flights were made, but these varied greatly in height. It is desirable to compare the insect catches of as many flights as possible with their differing weather conditions, but clearly we must not compare those taken from widely different height ranges. We may conveniently divide the series of flights into five arbitrary height ranges as follows:

Above 1000 ft.:	8	flights totalling	12·5 hr.
751–1000 ft.:	6	,,	10·25 ,,
501–750 ft.:	15	,,	19·75 ,,
251–500 ft.:	44	,,	69·5 ,,
150–250 ft.:	9	,,	12·25 ,,

In one height range alone, that from 250 to 500 ft., we have a sufficient number of flights to make a general correlation with weather conditions worth while. All the following correlations are confined to this series of 44 flights giving a total of 69·5 hr. collecting. The flights were usually of 1 hr. duration each, but sometimes they were longer and on a few occasions were less. Throughout the

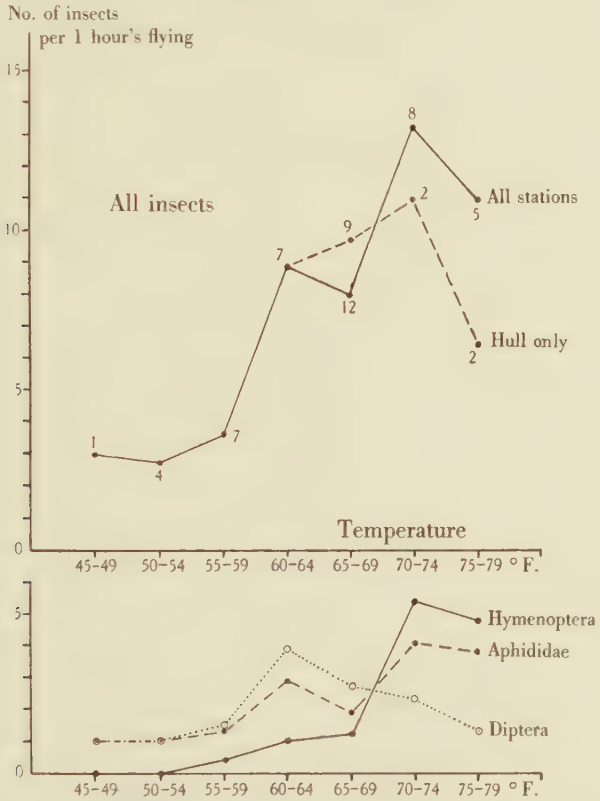

Fig. 5. Curves showing the average number of insects per 1 hr. collecting within the height range of 250–500 ft. at different ranges of temperature from 45–79° F. The numbers against the points on the curves represent the number of observations averaged in each temperature range. The Aphididae, Hymenoptera and Diptera curves are based on all stations; in the case of total insects the Hull observations are in addition shown separately.

following calculations the number of insects caught per flight have, where necessary, been converted to numbers per 1 hr. collecting.

Fig. 5 shows the correlation of the numbers of total insects, aphides, Diptera and Hymenoptera with a scale of temperature. The curves represent the average number of insects for the flights made within different temperature ranges; the numbers of flights averaged in each range are shown as figures against the curves. Of the 44 flights concerned 32 were made at Hull; of the remainder 4 were made at Thorpeness and 8 at Abbot's Cliff. In the case of the total

insects where the curve for the Hull flights differs from that of all the flights it is shown as a separate broken-line curve. Fig. 6 shows in a similar manner a correlation with a scale of percentage humidity. In the total insects we see clearly a general rise with temperatures up to 70–74° F., followed by a slight falling off of numbers at higher temperatures, and we see a general fall in numbers with increasing percentage humidity. The aphides show a moderate correlation with increasing temperature and a less regular inverse correlation

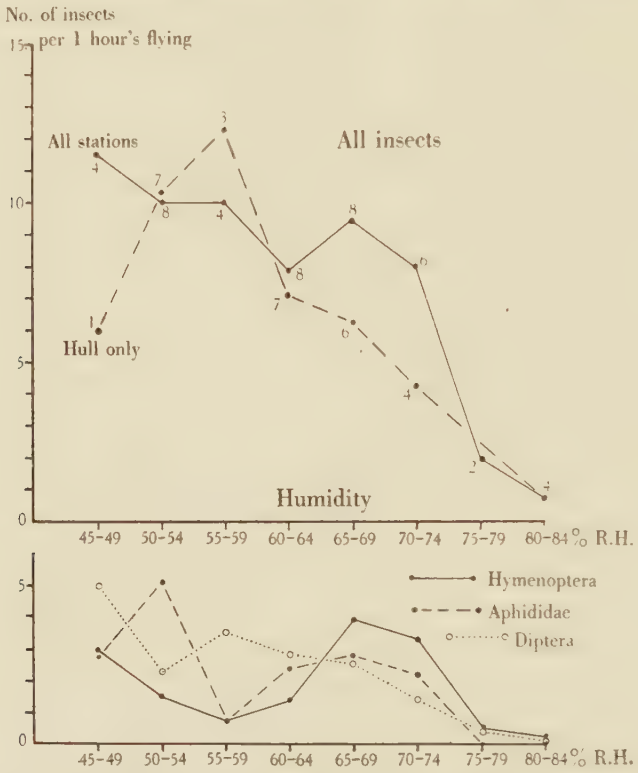

Fig. 6. Curves showing the average number of insects per 1 hr. collecting within the height range of 250–500 ft. at different ranges of percentage relative humidity from 45–84%. The arrangement is similar to that of Fig. 5 for temperature.

with increasing humidity. The Diptera appear to be more definitely correlated with humidity than with temperature and the Hymenoptera clearly the reverse.

Figs. 7–10 show the influence of temperature and humidity taken together on total insects, aphides, Diptera and Hymenoptera respectively. The dots in the figures represent the relation of the different flights to the two scales of temperature and percentage humidity. The numbers against each dot are the number of insects taken in each flight (per 1 hr. collecting). A thin horizontal line is drawn across the figure to separate 22 of the flights in a higher range of

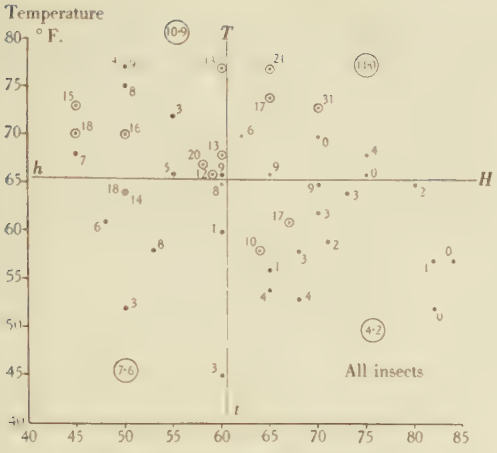

Fig. 7.

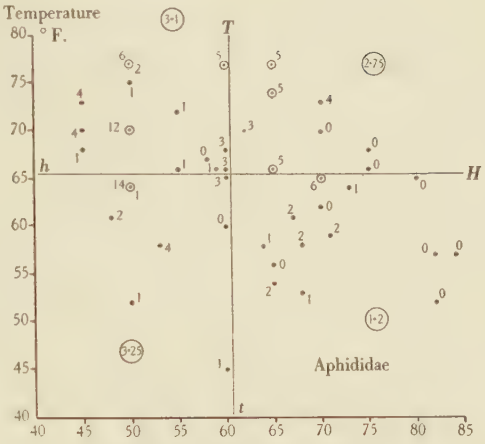

Fig. 8.

Fig. 7. Temperature-humidity diagram. The points in the diagram represent the position of each station within the 250–500 ft. height range in relation to the temperature and humidity scales. The number against each point stands for the number of insects taken per 1 hr. collecting at each station. When this number exceeds 10 the point is given prominence by being surrounded by a circle. The four numbers in circles represent the average number of insects per 1 hr. collecting taken within the area between the intersecting lines *Tt* and *hH* which divide the figure into regions of high and low temperature and humidity.

Fig. 8. Temperature-humidity diagram with similar arrangement as Fig. 7 but for Aphididae only, and with catches of 5 and over given prominence.

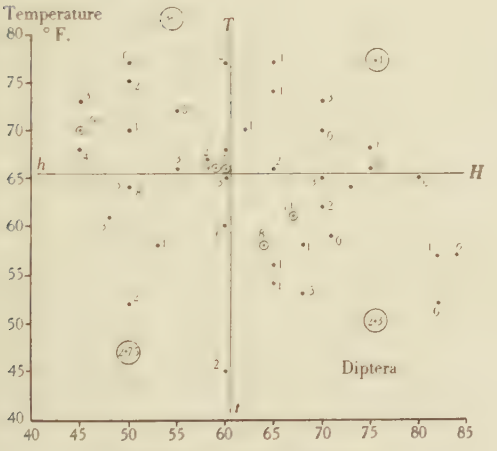

Fig. 9.

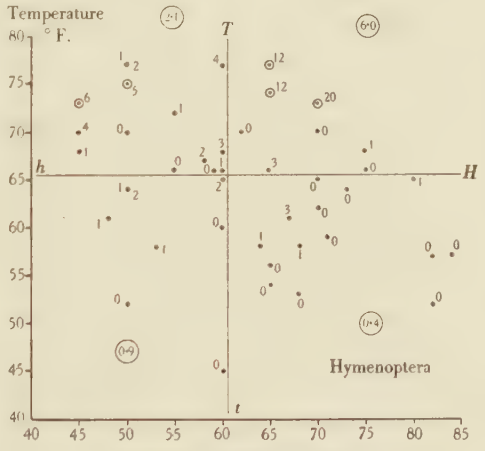

Fig. 10.

Fig. 9. Temperature-humidity diagram with similar arrangement as Fig. 8 but for Diptera only.

Fig. 10. Temperature-humidity diagram with similar arrangement as Fig. 8 but for Hymenoptera only.

temperature from 22 in a lower range of temperature; this line cuts the temperature scale at 65·5° F. Similarly, a vertical line separates 22 of the flights in a higher range of humidity from 22 in a lower range of humidity; this cuts the humidity scale at 60·5%. These two lines, *Tt* and *hH*, divide the figure into four regions which for convenience may be referred to as *Th*, *TH*, *th* and *tH* (*T* and *t* indicating high and low temperature, *H* and *h* indicating high and low humidity). It so happens that the contrasting squares *Th* and *tH* have each 14 observations in them, so that *TH* and *th* each have 8 observations.

We may now compare the average number of insects taken in each area. Let us first contrast the average number taken in the areas *Th* and *tH*:

	Th	*tH*
All insects	**10·9**	4·2
Aphididae	**3·1**	1·2
Diptera	**3·1**	2·3
Hymenoptera	**2·1**	0·4

We see in each case that *Th* is more favourable than *tH*. Now let us contrast *th* with *TH*.

	th	*TH*
All insects	7·6	**11·0** (9·0)*
Aphididae	**3·25**	2·75
Diptera	**2·75**	1·1
Hymenoptera	0·9	**6·0** (3·75)*

* Omitting 16 chalcids (i.e. 12 for ¾ hr. collecting at Station 43).

This latter comparison has not the same weight as that of the other pair of conditions, since these are based on only eight observations in each as against fourteen in the other pair. The same caution must be applied to the following consideration: if we refer across from one pair to the other we see that for each insect group *th* is more favourable than *tH* and that whilst *Th* is more favourable than *TH* for aphides and Diptera, it is not so for Hymenoptera and total insects. If we exclude the one high catch of chalcids at Station 43 then for the total insects *Th* > *TH*. These results are summarized graphically in Figs. 11–14. Here the lines *Tt* and *hH* cutting at right angles represent the lines *Tt* and *hH* in Figs. 7–10. The values for the average numbers of insects taken in the areas *Th*, *TH*, *tH* and *th* are plotted along the diagonals outwards from the point of their intersection. The plotted points are now connected to make polygons, which may be compared to give an indication of the respective behaviour of the different insect groups in relation to temperature and humidity. These figures based on only a small number of examples must be regarded as only a preliminary indication of the comparative trends.

Bright sunshine might be a factor influencing the flight of insects and so their passage to higher levels by rising currents, but on the present data it is not easy to separate the effect of sunshine from temperature and humidity. In Table 6 are given the average numbers of insects per 1 hr. collecting between

250 and 500 ft. when the conditions were sunny (b, bz, or bbc : 14 instances), partly sunny (bc, bcz: 16 instances) or cloudy (bcc, c: 13 instances). The average temperatures and percentage humidity for these conditions are also

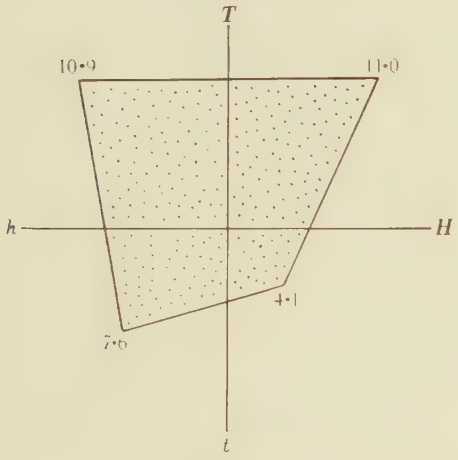

Fig. 11.

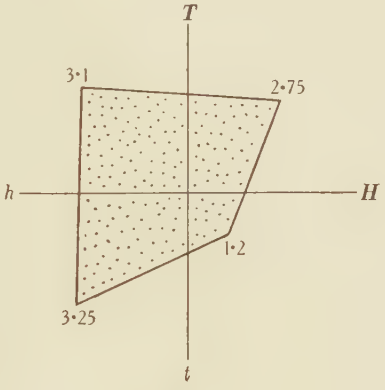

Fig. 12.

Fig. 11. Temperature-humidity relations for total insects (see text).
Fig. 12. Temperature-humidity relations for Aphididae (see text).

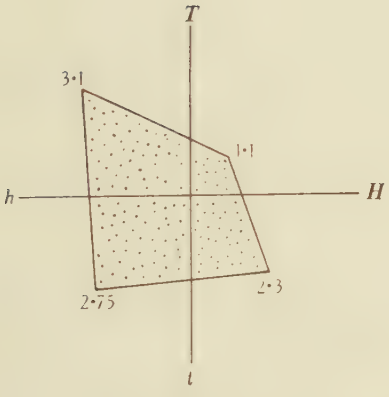

Fig. 13.

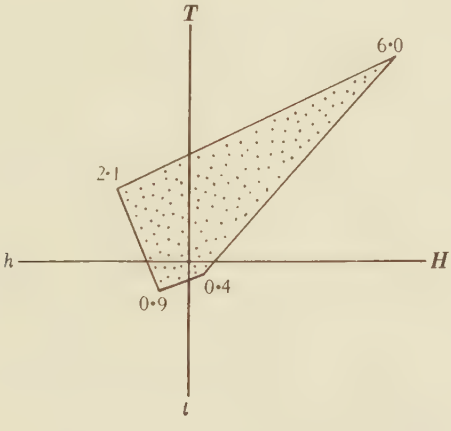

Fig. 14.

Fig. 13. Temperature-humidity relations for Diptera (see text).
Fig. 14. Temperature-humidity relations for Hymenoptera (see text).

given. Whilst we see that higher numbers are taken for all insect groups in sunshine, the accompanying temperature is highest and humidity lowest.

There appears to be no significant correlation between the numbers of insects taken and barometric pressure, as shown in Table 7, and there are not

sufficient data to make a correlation with wind force. The kites could not be flown in very light or high winds; the majority of flights were made in winds of force 3–4, only two flights in this height range (250–500 ft.) were in winds below force 3 and only four above force 5. Data on the influences of wind will be published by Mr Freeman in his forthcoming paper on the results obtained with nets flown on the masts of a wireless station.

Table 6. *Average number of insects per* 1 *hr. collecting under conditions of sunshine or cloud* (250–500 *ft.*)

	(b, bz, bbc)[14]	(bc, bcz)[16]	(bcc, c)[13]
Total insects	**11·6**	6·6	7·1
Aphides	**3·6**	2·3	2·5
Diptera	**3·1**	2·3	2·8
Hymenoptera	**4·6**	1·1	0·8
Av. temp. ° F.	**67·2**	64·4	62·3
Av. % humidity	58·6	62·4	**63·4**

Table 7

Barometric pressure in mb.	Average number of insects per 1 hr. collecting
<1010	8·3(3)
1010–1014·9	3·8(9)
1015–1019·9	10·7(13)
1020–1024·9	9·2(13)
>1024·9	7·2(6)

8. Estimates of the drifting insect populations

An early attempt to measure the density of the insect population of the lowest stratum of the air was made by Bonnet (1911), who made collections with a net attached to the front of a motor car. He found that the average density of the population at this level varied from 0 to 150 per cu.m. of air, depending upon time of day, temperature and humidity of the air.

Weiss, Felt and others (see Uvarov, 1931) studied the insects at slightly higher levels, and proved that the population of the respective strata of the atmosphere must be very rich in numbers, but the first estimate of the magnitude of the population was made by Coad (1931). He found that the number of insects in a vertical column of air 1 mile square and extending from 50 to 14,000 ft. above the ground averaged 25,000,000 throughout the year at Tallulah, Louisiana, the population being lowest in January at 12,000,000 and highest in May at 36,000,000. Details of the collections and the figures on which the estimates are based were not given[1].

In Table 8 is given the average number of insects taken per 10 hr. collecting with our kite-nets at various height ranges between 150 and 2000 ft. These results are shown graphically in Fig. 15, together with results kindly supplied to us by Mr Freeman from his collections in nets of similar size flown from the masts of the Tetney wireless station in Lincolnshire. The two sets of data form

[1] See Addendum note on p. 226.

Table 8

Height ranges in ft.	Hr. collecting	Average number of insects per 10 hr. collecting in a 3 ft. diameter net
1000–2000	12·5	44
750–1000	10·25	38
500–750	19·75	48
250–500	69·5	73
150–250	12·25	117

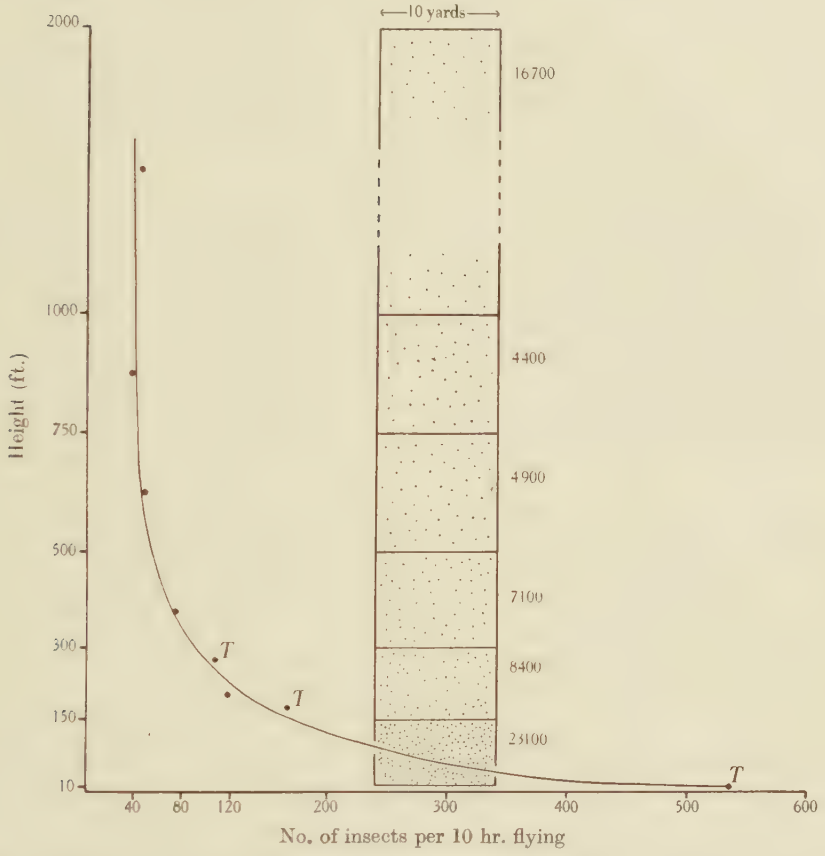

Fig. 15. Graphic representation of the density of the aerial plankton at different heights up to 2000 ft. The curve is based on the number of insects taken per 10 hr. collecting by kite-nets and at the points marked *T* by nets flown from the masts of the Beam Wireless Station at Tetney, Lincolnshire. In addition the average numbers of insects estimated to be drifting over a 10 yd. frontage in 1 hr. within different height ranges are shown by a system of dots, each dot representing 100 insects.

a regular curve and clearly indicate the average density of the aerial plankton from just above ground-level to 2000 ft. The rapid falling off in numbers between 10 and 300 ft. is most marked, yet the numbers at the higher altitudes are

considerable. Superimposed on the curve we also show relative population densities at different heights by a series of dots, each dot representing 100 insects drifting across a 10 yd. frontage in an hour within the different height ranges.

These results show us clearly how much aerial food there is available for swifts and swallows. The behaviour of these birds in respect to height of flight on different days, i.e. flying high on warm dry days and low on cooler damper days, is in accordance with the correlations we have found between temperature and humidity and the numbers of air-borne insects.

Berland (1935) makes a division between a more densely populated "zone terrestre" extending from 1 to 300 m. and a less densely populated "zone planctonique" from 300–5000 m.; but in a subsequent paper (1936) he would place this division between the zones much lower, not higher than 100 m. Our results agree well with this.

To compare with Coad's estimates we can express our results as numbers of insects within each height range in a column of air 1 mile square, estimated on a basis of an average wind velocity during our experiments of 12 m.p.h. This is done in Table 9, where also are given the estimated numbers of insects per 10^6 cu.ft. of air in each height range. Coad's estimates for the whole column of air from 50 to 14,000 ft. when converted into average numbers per 10^6 cu.ft give a minimum of 69 in January and a maximum of 92 in May. These estimates are very high compared with ours.

Table 9

Height ranges in ft.	Estimated number of insects in column of air 1 mile square	Estimated number of insects per 10^6 cu.ft.
1000–2000	245,000	9
750–1000	65,000	9
500–750	72,000	10
300–500	104,000	18
150–300	123,000	29
10–150	339,000	87

9. Economic importance of insect drift by wind

The results of these experiments, together with the collections made over the North Sea (Hardy & Milne, 1937), from which it was shown that insects may be carried for distances of more than 150 miles, would seem to indicate clearly the importance of convection currents and wind drift in the distribution of insect pests from one part of the country to another and the infection of this country by pests brought from the continent.

In the present experiments the grain aphis (*Macrosiphum granarium* Kby.) was taken on 12 occasions and reached a height of 1600 ft. Other aphides listed as agricultural pests by the Ministry of Agriculture and Fisheries were taken up to the following heights: *Capitosphorus ribis* Linn. (410 ft.), *Macrosiphum pisi* Kalt. (1600 ft.), *M. rosae* Linn. (380 ft.), and *Myzus persical* Subz. (650 ft.).

The thrips, *Kakothrips robustus* Uzel., was taken up to 450 ft.; and of the frit-fly (*Oscinus frit* Linn.) 33 specimens were taken on 12 occasions up to 600 ft.

10. Summary

1. The insects carried by convection currents and wind, the aerial plankton, are investigated between the heights of 150 and 2000 ft. by collecting nets carried up by kites. The nets are sent up closed, opened automatically at the desired height, and closed again at the end of the sampling period before being hauled down.

2. The equipment and methods of working are fully described.

3. Eighty-two samples were taken yielding a collection of 839 insects during a total flying time of 124·5 hr.

4. The aerial plankton is made up essentially of small or light-bodied insects with weak powers of flight but with relatively large wing surface compared with body mass.

5. The composition of the aerial plankton at different heights is determined and the height distribution of the different families compared. A list of species identified is appended.

6. The influence of weather conditions is examined. Different insect groups are shown to be affected somewhat differently, but high temperature and low humidity are found for all to be more favourable to aerial drift than the reverse conditions.

7. The average density of the drifting population is estimated for different height ranges up to 2000 ft.

8. The economic significance of insect drift is discussed.

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ADDENDUM

Since going to press we learn that Dr P. Glick has made a detailed study of all the material collected on the flights initiated by Dr Coad (see pp. 200, 215 and 222) and that his results are now ready for publication.

APPENDIX

Table 10. *List of species identified in the collections* 1932–5. (*Only a few of the insects collected in* 1935 *have been determined specifically.*) *The names of the specialists responsible for the identifications in different groups are given on p.* 201. *The species listed as pests by the Ministry of Agriculture and Fisheries are marked with an asterisk*

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
PSOCOPTERA		
Pterodela pedicularia Linn.	49 (1)	500–1200
THYSANOPTERA		
Frankliniella intonsa Trybom	36 (1♀), 39 (1♀), 46 (1♀), 60 (1♀)†	250–2100
F. tenuicornis Uzel.	36 (1♀), 58 (1♀), 59 (1♀)‡	380–630
**Kakothrips robustus* Uzel.	30 (2♂), 58 (1♀)	400–500
Limothrips cerealium Halid.	36 (2♀), 52 (1♀), 59 (1♀)	250–630
L. denticornis Halid.	52 (1♀)	250–350
Sericothrips staphylinus Halid.	44 (1♀)	450
HEMIPTERA		
Lygaeidae		
Cymus claviculus Fall.	48 (1)	450–600
Jassidae		
Athysanus plebejus Fall.	48 (1)	450–600
Cicadula sexnotata Fall.	9 (1), 14 (1), 16 (1), 17 (1), 23 (1), 39 (1)	325–480
Deltocephalus pascuellus Fall.	42 (1)	350
D. pulicaris Fall.	35 (1), 77*a* (1)	400–1400
D. socialis Flor.	43 (1)	450
D. striatus Linn.	79 (1)	550–2000
Limotettix quadrinotata F.	45 (1)	250–350
Mocydia crocea H. S.	47 (1)	350–600
Stictocoris preyssleri H. S.	48 (1)	450–600
Delphacidae		
Kelisia vittipennis J. Shulb.	43 (1)	450
Liburnia pellucida F.	5 (1), 30 (1), 44 (1)	450–500

† Contained an egg ready to be laid. (Note by E. R. Speyer.)
‡ The posterior margin of the 8th abdominal tergite is indistinct, so that the insect might possibly (but improbably) be *F. intonsa* Trybom. (Note by E. R. Speyer.)

Table 10 (*cont.*)

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
Psyllidae		
Aphalara calthae Linn.	13 (1), 23 (4), 49 (1)	500–1200
Psyllia nigrita Zett.	36 (1), 44 (1)	450–630
Aphididae		
Anoecia corni Fab.	39 (1), 44 (1), 60 (1)	1600–2100
Anuraphis helichrysi Kalt.	2 (2), 9 (1), 23 (5), 27 (1), 28 (11), 30 (7), 31 (3), 32 (5), 37 (4)	450–610
Anuraphis sp.	9 (2), 39 (2), 41 (1), 42 (1), 47 (1)	350–600
**Capitophorus ribis* Linn.	37 (1)	410–610
Drepanosiphum platanoides Sch.	3 (1), 19 (3), 23 (2), 30 (2)	450–500
Euceraphis betulae Linn.	2 (2), 4 (1)	250–300
Hyadaphis sp.	32 (1)	200–500
Hyalopterus sp.	31 (1), 37 (1), 60 (1)	1600–2100
**Macrosiphum granarium* Kby.	15 (1), 28 (1), 30 (1), 36 (2), 37 (1), 38 (1), 43 (1), 44 (7), 47 (1), 48 (1), 59 (3), 60 (1)	1600–2100
M. pelargonii Kalt.	20 (1), 22 (1), 31 (1), 32 (1), 34 (1), 35 (1), 60 (7)	1600–2100
**M. pisi* Kalt.	36 (1)	380–630
**M. rosae* Linn.	32 (1)	200–500
Megoura viciae Kalt.	39 (1), 40 (1), 44 (1)	450–480
Myzocallis sp.	34 (1)	300
**Myzus persicae* Sulz.	26 (1), 44 (1)	450
	68 (1), 70 (1)	650
Myzus sp.	34 (1)	300
Pemphigus bursarius Linn.	18 (1), 44 (1)	450
Periphyllus sp.	28 (1)	250–350
Rhopalosiphoninus tulipella Theob.	28 (1)	250–350
Therioaphis tiliae Linn.	36 (2)	380–430
NEUROPTERA		
Conopterygidae		
Conwentzia psociformis Curt.	44 (1)	450
LEPIDOPTERA		
Pieridae		
Pieris rapae Linn.	59 (1)	450–500
COLEOPTERA		
Staphylinidae		
Atheta analis Grav.	31 (1)	200–300
A. angustula Gyll.	3 (1)	250
A. nigripes Thoms.	21 (1)	300–350
Exaleochara morion Grav.	2 (1)	150–200
Oxypoda umbrata Gyll.	13 (1)	250–300
Oxytelus nitidulus Grav.	1 (1), 2 (1), 4 (1)	250–300
O. rugosus F.	3 (1)	250
Philonthus varius Gyll.	74 (1)	400–1000
Tachyporus chrysomelinus L.	41 (1)	150
T. hypnorum F.	41 (1)	150
T. pusillus Grav.	21 (1)	300–350
Hydrophilidae		
Helophorus brevipalpis Bed.	4 (1)	250–300
Chrysomelidae		
Longitarsus luridus Scop.	43 (1), 75 (1), 76*a* (12), 76*b* (8), 78 (1)	950–2350
L. suturellus Duft.	77*a* (1)	400–1400

Table 10 (*cont.*)

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
HYMENOPTERA		
Ichneumonoidea		
Aphidius sp.	2 (1), 9 (1), 28 (1), 35 (1), 36 (6), 37 (3), 39 (1), 40 (1)	480–630
Biosteres rusticus Hal.	15 (1)	200–350
Blacus ruficornis Nees.	40 (1)	480
Canidia sp.	36 (1), 44 (1)	450–630
Dacnusa areolaris Nees.	34 (1)	300
Ephedrus plagiator Hal.	37 (1), 44 (1)	450–610
E. validus Hal.	18 (1), 35 (1), 39 (1)	350–480
Gyrocampa affinis Nees.	9 (1)	200–300
Hemiteles necator Grav.	18 (1)	350–400
Homotropus sp.	36 (1)	380–630
Chalcidoidea		
Aphidencyrtus aphidivorus Mayr.	12 (1)	250–300
Asaphes vulgaris Walk.	14 (1), 21 (1), 22 (1), 36 (2), 45 (1), 46 (1)	600–630
Cirrospilus sp.	34 (1), 36 (1), 40 (1), 44 (1), 46 (1)	600–630
Cyrtogaster vulgaris Walk.	37 (1), 47 (1)	410–610
Pachyneuron sp.	23 (1), 49 (1)	500–1200
Panstenon oxylus Walk.	39 (1)	280–480
Pleurotropis sp.	15 (1), 37 (1), 43 (2), 44 (1)	450–610
Pteromalus sp.	36 (1), 43 (7), 44 (2), 47 (2)	450–630
Stenomalus sp.	43 (1), 48 (1)	450–600
Tetrastichus sp.	36 (1)	380–630
Cynipoidea		
Alloxysta filicornis Cam.	36 (2), 37 (2)	410–630
Alloxysta sp.	37 (1)	410–610
Charips victrix Westw.	36 (2), 37 (2)	410–630
Proctotrypoidea		
Conostigmus dubiosus K.	49 (1)	500–1200
Conostigmus sp.	43 (1)	450
Lygocerus aphidivorus Kieff.	15 (1)	200–350
L. serricornis Bov.	36 (1)	380–630
Lygocerus sp.	36 (1), 43 (1)	450–630
Platygaster mayetiolae K.	36 (1), 37 (2), 40 (1)	480–630
Trichosteresis försteri Kieff.	38 (1)	150–410
DIPTERA		
Mycetophilidae		
Sciara spp.	1 (19), 2 (15), 3 (5), 4 (5), 5 (8), 6 (3), 13 (8), 16 (1), 18 (2), 20 (2), 21 (4), 24 (1),	500
	27 (1), 28 (2), 31 (2), 32 (1), 39 (3), 44 (1), 49 (1), 52 (4), 54 (1), 69 (1), 79 (2)	600–2000
Bibionidae		
Dilophus febrilis L.	26 (1)	200–450
Cecidomyidae		
Camptomyia sp.	34 (1)	300
**Contarinia* spp.	26 (1), 32 (1)	200–500
Chironomidae		
Metriocnemis longitarsus Goet.	4 (1)	250–300
Tanytarsus sp.	49 (1)	500–1200
Psychodidae		
Psychoda phalaenoides L.	6 (1)	250–350

Table 10 (*cont.*)

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
Rhyphidae		
Rhyphus punctatus Fab.	1 (1)	150–200
Tipulidae		
Trichocera saltator Harris	24 (1)	350–375
Empididae		
Tachydromia sp.	2 (1), 20 (1), 48 (1)	450–600
Lonchopteridae		
Lonchoptera lutea Fall.	43 (1)	450
Phoridae		
Megaselia sp.	21 (7), 48 (1)	450–600
Agromyzidae		
Agromyza scutellata Fall.	44 (1)	450
Agromyza sp.	48 (1)	450–600
Cerodonta denticornis Pz.	32 (1)	200–300
Phytomyza flava Fall.	10 (1), 11 (1), 17 (1)	300–350
Chloripidae		
**Oscinis frit* Linn.	10 (1), 13 (1), 15 (2), 18 (2), 20 (1), 21 (1), 44 (4), 45 (1), 46 (3), 47 (11), 48 (4), 52 (2)	600
Siphonella sp.	40 (1)	480
Cordyluridae		
Scatophaga stercoraria L.	11 (1), 12 (1)	250–350
Drosophilidae		
Drosophila fenestrarum Fall.	20 (1), 21 (1), 43 (1)	450
Scaptomyza graminum Fall.	40 (1), 41 (1)	480
Ephydridae		
Hyadina guttata Fall.	34 (1)	300
Hydrellia incana Stenh.	5 (6), 8 (1), 9 (2), 16 (2), 17 (1), 20 (2), 34 (1), 76*b* (1)	300–350
Scatella stagnalis Fall.	21 (1), 36 (2), 37 (1), 76*a* (1)	850–1250
Sepsidae		
Sepsis cynipsea L.	41 (1)	150
Sphaeroceridae		
Copromyza equina R. D.	24 (1), 30 (1)	450–500
C. hirtipes R. D.	21 (2), 23 (1)	325–375
Leptocera fontinalis Fall.	21 (1)	300–350
Leptocera spp.	13 (1), 21 (3), 22 (1), 23 (1), 38 (1), 44 (1)	450
Muscidae		
Delia sp.	1 (1)	150–200

MIGRATIONS OF THE SILVER-Y MOTH (*PLUSIA GAMMA*) IN GREAT BRITAIN

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(*With 7 Figures in the Text*)

1. Introduction

Whenever the factors influencing the size and composition of animal populations are under consideration, the possibility of migration from one area to another should not be overlooked. This is usually recognized fully enough in the case of birds and mammals, but it is too often neglected in the case of insect faunas.

None the less, in the sense of the apparently wilful movement of large numbers of individuals for long distances independently of the direction of the wind, migration has been observed in several orders, notably in Lepidoptera and Odonata.

One reason for past neglect of the subject lies in the fact that many entomologists have found it difficult to believe that insects possess the intricate mental or instinctive organization necessary to enable them to undertake deliberate migrations, and so have never looked out for them. As a result, migrations have only been recorded when they have been dense enough to force themselves on the attention of all who came in contact with them. In temperate climates they tend to be ignored altogether, being usually thin and inconspicuous, although careful observation shows them to be frequent.

During the past few years, the situation has much improved. An Insect Immigration Committee has been set up by the South Eastern Union of Scientific Societies, and, thanks largely to the energy and enthusiasm of its Secretary, Capt. Dannreuther, R.N., it is now receiving help from naturalists in all parts of the country, including the keepers of many lighthouses and lightships. Since the majority of the observers are amateurs, Lepidoptera have naturally received the most attention, and as far as some of the species belonging to this order are concerned, fairly solid progress has already been made in various directions.

British migratants have been divided into three groups, according to their relationship to permanent fauna:

Class A. Species which are unable to pass the winter here, but which appear every summer. They only occur in Great Britain as a result of their migratory habit, and would disappear from the fauna should the migrations cease. Example: *Vanessa cardui* L.

Class B. Species which survive the winter and form part of the normal fauna, but whose numbers are reinforced by immigration. Example: *Pieris rapae* L.

Class C. Species which are normally absent, but which may occur occasionally as vagrants. Example: *Argynnis lathonia* L.

These divisions have been found useful, but they are by no means final; Classes A and B, for example, having a tendency to merge into one another. The difference between Classes A and C, however, does seem to correspond roughly to two different types of migration, though certain insects may behave as Class C in this country which are Class A elsewhere.

As a result of the information so far collected by the Insect Immigration Committee, it begins to look as if the movements of the Class A insects correspond very closely with those of swallows and similar birds. The species concerned appear regularly every spring in considerable numbers, and breed in

Natural size

Fig. 1.

this country. Their offspring reach maturity in late summer and autumn, and in many if not most years the autumn emergences are more numerous than the spring arrivals. Finally in some of the Class A species, *a return flight southwards seems to occur in autumn*, making the migrations a normal and intelligible part of the life of the species, instead of an inexplicable aberration.

The other type of movement, represented by Class C, is more like that of the lemmings. Arrivals are very irregular, and may take place only at long intervals. A British born generation may or may not reach maturity; no return flights are to be expected, and the "migration" would seem to be nothing more than an overflow of surplus population from the normal breeding area.

The present paper is an attempt to deal with a Class A migrant, and while the results so far obtained are not conclusive, they are at least consistent with the suggestions put forward above.

The silver-Y moth, *Plusia gamma* L., has been chosen for this study largely because of the amount of attention it has received from observers under the

Insect Immigration Scheme. It is one of our commonest Lepidoptera, is easy to recognize, and is familiar to every entomologist, yet it is practically never recorded in winter time. Very rarely single specimens have been caught as late as November, like solitary late swallows, but although swarming thousands may be present at the beginning of October, they disappear suddenly about the middle of the month, and except for occasional solitary individuals in November not a trace of them is seen again until the following spring.

There seems to be no doubt that the vast majority of individuals emerge from the pupa in late summer or autumn, and that the winter is passed in the imaginal form. It is exceptional for oviposition to take place in autumn, and all females sent to me for dissection late in the year have had minute ovaries with undeveloped eggs and a copious fat body, characteristics of a species which is to pass the winter in the adult state and will not be ready for oviposition until long after most of the food plants have died down for the winter. If, therefore, the species was not a migrant, but remained in Great Britain, we should expect the majority of insects caught during the winter to be in the adult form and not in the pupal state. This, however, is not the case. Winter records have been especially asked for by the Insect Immigration Committee; only two have been received of insects found from January to April during the past six years, and both of these were pupae. It is difficult to obtain information about the life history of the species abroad, but it is believed to be continuously brooded in warmer climates.

2. Distribution in Great Britain from 1932 to 1936

The information received from the Insect Immigration Committee during the past five years may conveniently be summarized in this section; distribution in three years is illustrated in Figs. 2 (1934), 3 (1935), 4, 5 and 6 (1936).

1932. The first *P. gamma* to be reported in 1932 was seen in Beckley, Sussex, on 19 May, and the main body of immigrants appeared about three weeks later. During June and July moderate numbers were seen in southern England, and as far north as the south Lancashire coast; emergence of the summer generation appears to have begun about the first week in August. Even when allowance is made for the fact that the Insect Immigration Scheme was still in its infancy in 1932 and that observers were fewer than in later years, this emergence does not seem to have been much more numerous than the spring migrants except in one or two places in the south, where the moths were common in August. By the end of the month they had already begun to decrease in number, though a few were seen well on into October, and a single individual was reported from Worcestershire as late as 3 November. No directional movements were recorded in 1932.

1933. The first immigrant was seen on 4 May, a fortnight earlier than in the previous year, and the summer generation was also rather early, emergences taking place from 15 July on. Nevertheless, the year was a bad one for the

species as a whole, and the moths were only seen in numbers in one or two restricted localities. The most northerly point from which they were reported

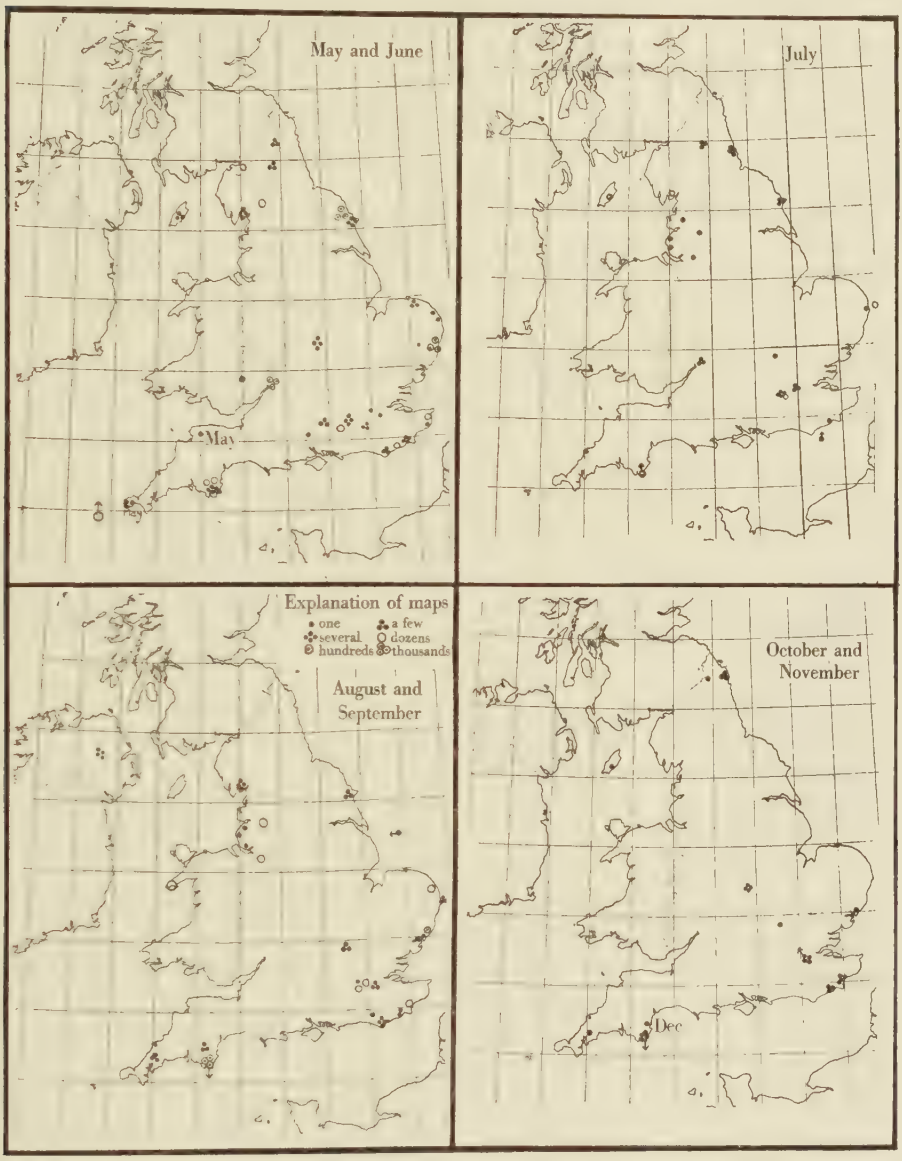

Fig. 2. Distribution of *Plusia gamma* in 1934.

was Annan in Dumfriesshire but, as in the previous year, this may have been due rather to a lack of observers further north than to actual absence of the species. Only a few scattered individuals were seen in September, and the last moth was seen in Devon on 23 October, the earliest last date that has been

recorded since the work began. Only two directional movements were recorded; six moths were observed from the East Dudgeon Light Vessel (24 miles out to sea, north of Hunstanton, Norfolk) while making their way westwards on 7 July; fourteen more, also flying towards the west, were seen in Barrow-on-Soar on 11 September.

1934. Records of *P. gamma* were far more numerous in 1934 than in previous years. This may have been partly due to the greater number of observers taking an interest in migration, but the fact that individual observers saw more moths at a time than they had in previous years shows that the species itself was more common. The season was a late one as a whole. The earliest arrival was seen on 28 May, and the main body of immigrants reached England at the beginning of the last week in June, when the species became very common in many places in the south, and was reported singly as far north as Unst in the Shetland Isles. (These last records are not shown in Fig. 2.) About this time a large immigration seems to have reached the extreme west of England from the south, perhaps from Spain via the Bay of Biscay. They were first observed in the Scillies, where dozens of them were seen flying north in the late afternoon of 22 June by Mr R. Trotter of the Round Island Lighthouse. Three days later they were seen in hundreds in several places in Gloucestershire and on the Welsh Borders; by 1 July they had disappeared from these localities, and further evidence of their movements is lacking. From Devon to east Kent the species was numerous by the end of June, and oviposition was reported from Dartmoor on 27 June.

Immigration from the south continued very late in 1934, since moths were seen coming in from the sea in south Devon on 21 July, and in the Channel near Folkestone on the following day. Only one moth was seen flying westwards in August; but as that was observed 30 miles out to sea off the east coast (Outer Dowsing Light Vessel), even by itself it is a faint indication of migration in this direction. On 12 September Mr A. W. Godfrey, of the Start Lighthouse, near Hallsands in south Devon, saw a large migration going out to sea southward between 9 and 11.30 p.m. Many of the moths were attracted to the light and rested on the glass of the lantern, so he was able to secure a number of specimens for identification. This experience of southward migration was repeated on 23 September and 2 October at the same place, but on these occasions the numbers were much smaller.

The moths continued to increase in number until mid-September, although they were never so common as they had been in spring. At the end of the month they began to decrease rapidly; only two individuals were seen after the third week in October, but one of these was exceptionally late (3 December). No more moths were seen from then until the following May.

1935. Much more regular observations were made in 1935 than in previous years, especially in Hastings, where Mr H. G. Macleod took nightly counts throughout the summer. These observations, which are most valuable, have

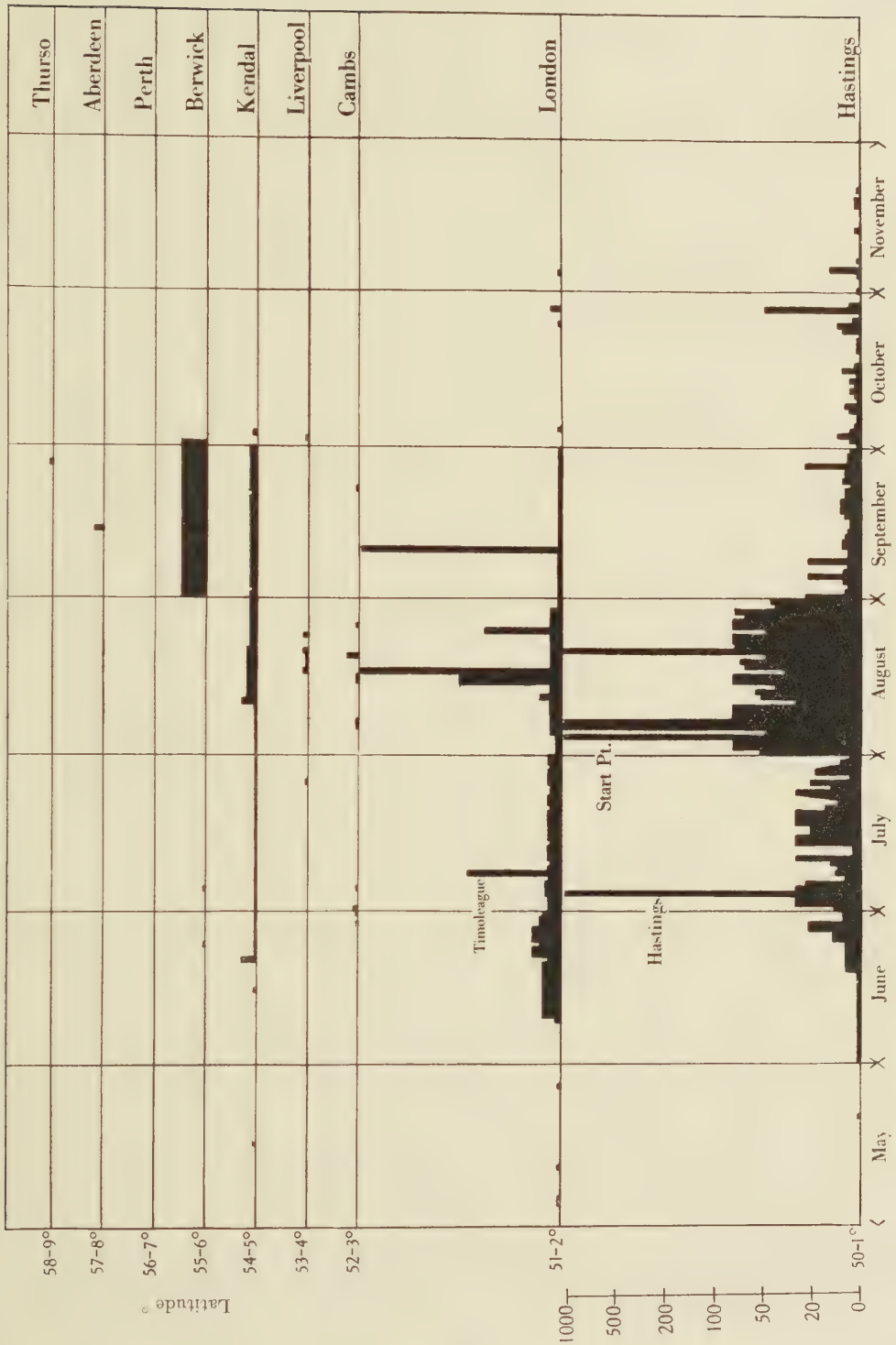

Fig. 3. Distribution of *Plusia gamma* L. in 1935.
(Vertical scale = av. no. seen per observer per day.)

been continued ever since. The form of graph used in Figs. 3 and 6 to illustrate the distribution in this year and in 1936 needs some explanation. The graph is

Fig. 4. Distribution of *Plusia gamma* in 1936.

divided into horizontal strips, each one of which represents a degree of latitude. In the 1935 graph, the lower strips are wider than the others, to accommodate the greater number of insects recorded from the southern counties: the vertical

scale of abundance is the same. The vertical column represents the average number of insects seen per observer each day. Since the number of observers

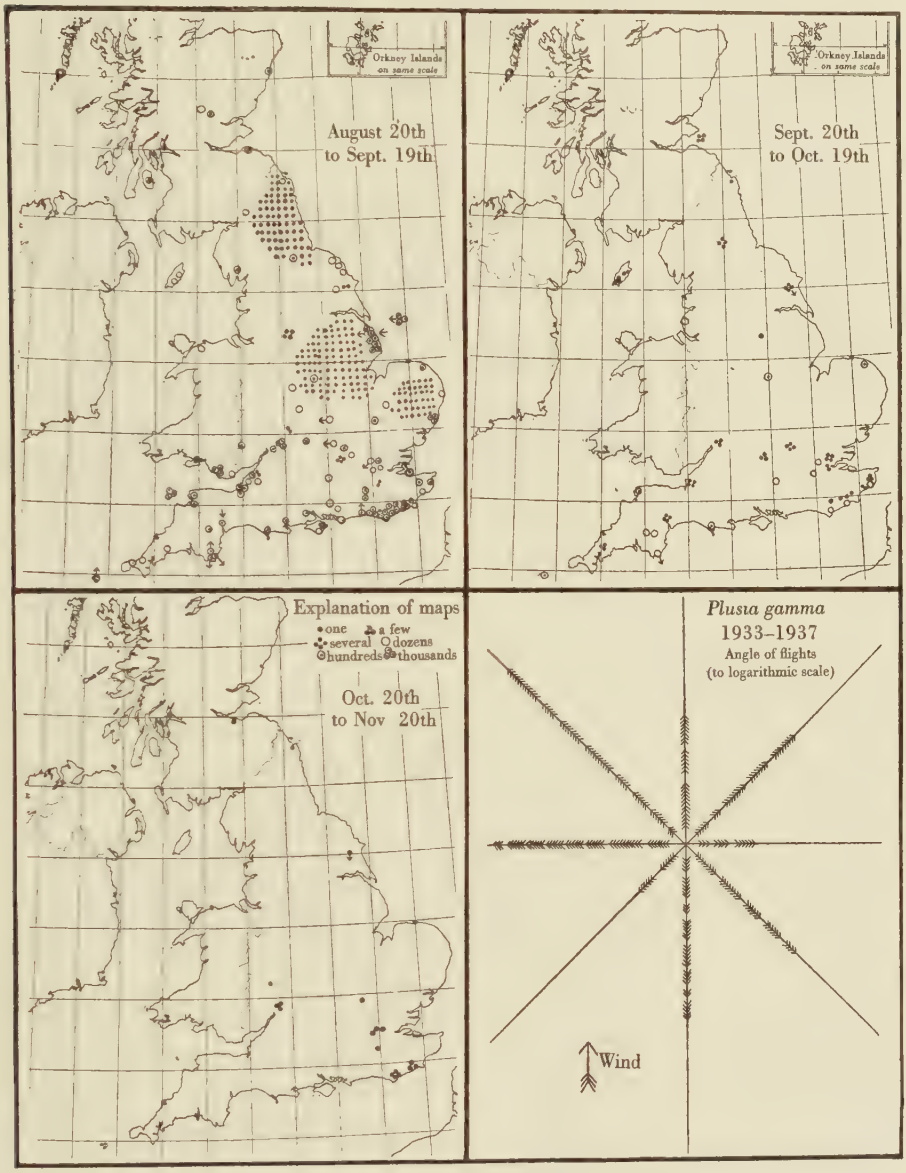

Fig. 5. Distribution of *Plusia gamma* in 1936.

decreases rapidly towards the north, a direct addition of all moths recorded per day in each degree would result in an exaggeration of the numbers seen in the south; this error is largely obviated by averaging the number per observer.

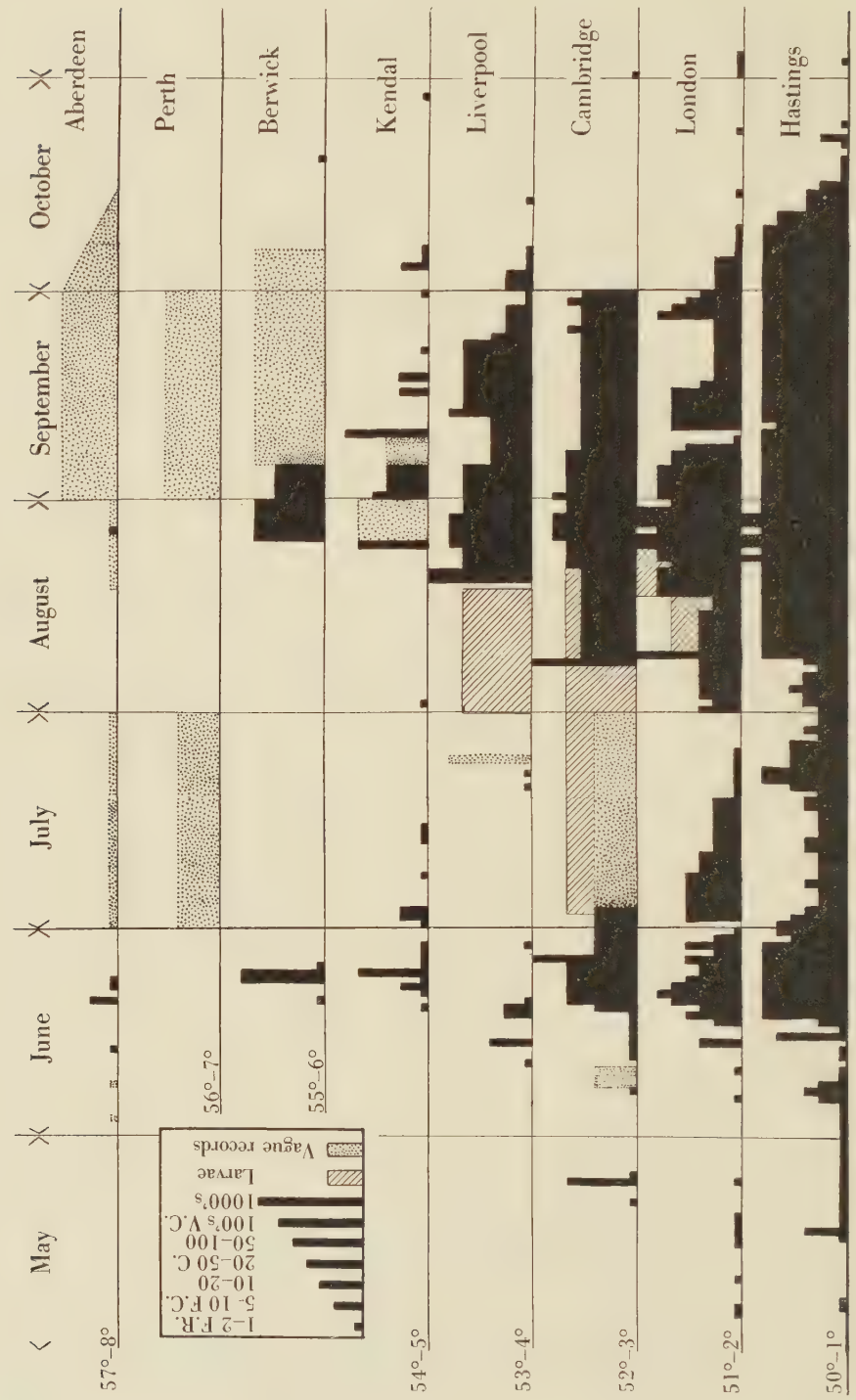

Fig. 6. Distribution of *Plusia gamma* in 1936.

The number seen in the south is still greater than in the north, but this is a real effect and does not depend on the number of observers.

The first moth seen in 1935 was recorded in Timoleague (Ireland) on 5 May. Maximum summer emergences also took place earlier than in 1934, quite large numbers being counted in August; a large southward migration from the Start was witnessed on the 4th of that month. The moths had a considerable northward range, being reported from the extreme north of Scotland; but on the whole they were uncommon except in the south. In one or two places they appeared in large numbers, but as this was only for one or two days at a time, it is probable that these were migrations passing through. A few solitary moths were again seen flying westwards in August from the Outer Dowsing Light Vessel (30 miles to the east of Spurn Head), in this case after the southward emigration of British bred moths had begun. Numbers decreased very suddenly at the beginning of September over most of the country, though it appears as if an emergence had taken place in southern Scotland about this time. A few moths lingered on until the beginning of November and one solitary individual was seen in Hastings on the 21st of that month.

1936. This was perhaps the most remarkable *P. gamma* year ever fully recorded. The species was extremely common and widespread, and was seen as far north as Fair Isle (Shetland). In some parts of southern England the moths were so numerous that observers gave up attempting to estimate their numbers in thousands and reported them in "myriads". A curious feature of the summer distribution, noticeable in other years, but emphasized in this year of plenty, is the great variation in numbers between neighbourhoods quite close to one another. This may perhaps be attributable to gregariousness, since the migrations of *P. gamma* frequently seem to include much greater numbers of individuals than do flights of most of the other regular migrants in this country. Harpenden, in Hertfordshire, seems to be one of the places where the species is regularly less common than elsewhere. Here at Rothamsted a light trap has been run nightly over the greater part of the period dealt with in this paper, and personal observations have also been made during daylight. Yet, in 1935, at a time when a light trap only a few miles away on the Buckinghamshire-Bedfordshire border was catching as many as 400 *P. gamma* in one night, only solitary individuals were seen in Harpenden, and in 1936, when the moths were reported in thousands all over the country, the largest count made near Harpenden was a little over a hundred, and that only on one day and after considerable search.

1936 was a fairly early year. The first migrant was seen in Croydon on 6 May, and immigrants were seen flying northwards in late May and June. During the latter month swarms of moths reached the sugar-beet fields of Lincolnshire and Norfolk in such numbers that the sound of their wings was audible as a distinct humming, and the crops were damaged later by the resulting larvae. Extensive breeding also probably took place in northern

Europe, since flights westwards across the North Sea reached enormous proportions in August. During the first three weeks of August these westerly movements predominated; from the end of that month until October flight direction was chiefly towards the south. There was a certain amount of overlap between these two flight directions, however, and the position was further complicated by several definite immigrations of quite large numbers of the moths from the south. During October the number of moths present in Great Britain decreased fairly rapidly, but a few persisted until the end of that month, and occasional individuals were seen until the end of November.

1937. Up to the end of September very few records for this year have as yet come to hand. As far as can be ascertained, the moths have been definitely uncommon everywhere, both in spring and summer. Three southward migrations have, however, again been seen at the Start Lighthouse, all during August; two of these movements were comparatively thin, but one comprised some thousands of moths.

3. Seasonal variation of flight direction

Fig. 7 is intended to show how the direction of flight in *P. gamma* varies during the summer, and was made by combining all the flights in which direction was recorded from 1933 to 1937 (no directional flights were reported in 1932). Each separate flight is represented by a group of darts pointing in the appropriate compass direction, and even single individuals have been included. The flights vary greatly in number, from one to many thousands, and for convenience in representation a logarithmic scale has been used. Thus,

1	dart	represents	1 moth
2	darts	represent	2 moths
3	,,		5 ,,
4	,,		10 ,,
5	,,		21 ,,
6	,,		46 ,,
7	,,		100 ,,
8	,,		210 ,,
9	,,		460 ,,
10	,,		1000 ,,

and so on, so that a large number of small flights tends to show a similar importance to a small number of large flights. This is designed to effect a compromise between putting in a dart for each insect, which is impossible for reasons of space, and putting in a dart for each flight, which would altogether exaggerate the importance of solitary insects which may or may not have been migrating when recorded.

It will be seen from the summary of records for the past five years that solitary moths begin to appear in May, after an absence of five months. They

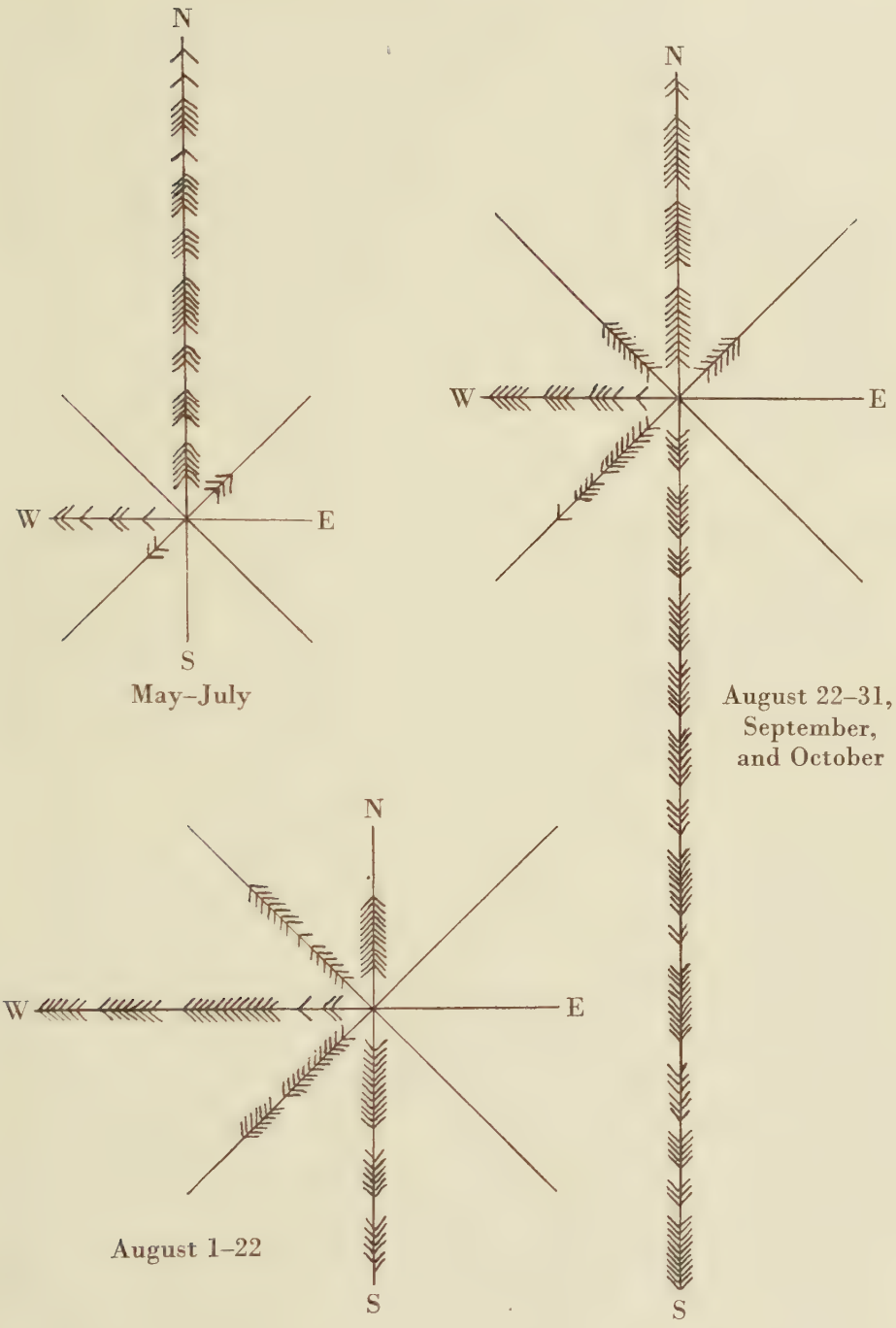

Fig. 7. Directional flights of *Plusia gamma* from 1933 to 1936, with a few flights of 1937.

are followed by gradually increasing numbers through May and June, the maximum number of immigrants being reached five or six weeks after the first appearance. During this period the direction of flight is predominantly northwards. In July, although some immigration may occur, the majority of the moths lay their eggs and die, and the number of adult moths seen is considerably reduced (Figs. 3 and 6). The emergence of the adult generation usually occurs in August, though it may begin as early as July, or be retarded until September. There seems to be some connexion between the time of arrival of the first immigrants and the time of emergence of the British bred moths: if the first is delayed, the latter is late also. In four years out of five, westerly migrations have been observed, the moths entering Great Britain across the North Sea from some unknown point further east. This westerly movement is preponderant in early August, though it may occur as early as June or as late as September.

The moths which emerge in summer commence to feed upon the nectar of flowers, and being active by day as well as by night, may be observed to fly and to feed greedily in bright sunshine. Such females as have been dissected in autumn have their ovaries small and eggs undeveloped, and both sexes have copious fat bodies. From late August onward flight direction is preponderantly south, though there may be overlapping of westerly and southerly flights. In an unusually early year, large numbers may emigrate in the beginning of August, as in 1935. Immigrations from the south may take place in late August, at the same time that British bred moths are moving in the opposite direction; these flights, however, are probably to be regarded as exceptional.

4. General factors influencing migration

The actual commencement of a migratory flight of *P. gamma* has twice been witnessed in this country, once by the late Robert Adkin on the Downs behind Walmer in Kent, and once by Mr L. W. Newman (*in litt.*), at the foot of the hills near Folkestone. Mr Newman saw the moths rise from a field at dusk in a spiral and make for the sea; the time was late September. Adkin (1920) also saw the moths fly upward from a field in the evening; but in this case, although great numbers were seen to rise from the corn, they flew so high that they went out of sight and it was impossible to distinguish the direction in which they eventually flew. The evening was warm and calm and it was still light.

If the place and time of commencement of all observed migrations were known, very interesting correlations with weather conditions might be made. In the absence of direct evidence, however, it is possible to trace lines back across the map in the direction from which flights have come, and to select the most likely points on these lines for their possible origins (i.e. in the case of immigrants, the nearest point across the Channel). Weather records for the selected areas can then be obtained, and correlation attempted. If the results

Table 1

Observations of flight in progress				Conditions at possible starting place of migration				
Date	Place	No. of insects	Direction of flight	Date	Place	Barometer	Thermometer	Wind
1933								
7 June	East Dudgeon Lightship	6	W.S.W.	4–6 June	North Friesland	Falling to 6th, rising	Variable	S.E. then N.E., gentle
1934								
22 June	Round Island Lighthouse, Scilly	Dozens	N.	19–21 June	North-west Spain	Falling slowly	Slight rise	Calm
12 Sept.	Start Lighthouse, South Devon	Very large numbers	S. out to sea	10–12 Sept.	South Devon	Rising slowly	Rising slowly	Mainly light S. or S.W.
1936								
18 May	Hastings	Over 50	N. in from sea	15–18 May	Dieppe district	Falling 15–16, rising 17–18	Rising, then steady	Light variable
8 Aug.	Haisbro' Lightship	Dozens	N.W.	5–8 Aug.	Zeeland	Rising generally	Slight rise on 7th	Moderate S.W., veering N.E.
20 Aug.	Outer Dowsing Lightship	Many thousands	W.	17–19 Aug.	East Friesland	Falling a little on 19th	Falling	S.E. or S. light airs
24–30 Aug.	Exmouth	Hundreds	S.	22–28 Aug.	South Devon	Rising	Rising or steady	N. or N.W. fresh, falling calm

are at all regular and seem to show some connexion between migrations and weather factors, we may consider our original assumption as to starting points of the flights to be justified.

About fifty flights recorded under the Insect Immigration Scheme have been examined in this way, and the Meteorological Office have been kind enough to supply relevant weather records for the three days preceding each flight. Since the actual time of departure is unknown, there is no advantage in obtaining the exact figures for temperature and pressure; attention has only been given to whether the thermometer and barometer were rising, falling, or remaining steady during the period preceding the flights. Flights containing only one or two individuals have been neglected. Table 1 illustrates the way in which the available evidence has been gathered together: the first four columns show some of the particulars observed while the flights were in progress, while the remaining five columns show the conditions which prevailed in the Continental districts chosen. Where considerable fluctuations of pressure or temperature occurred, the conditions of the last day before the flight have been used in making the tables.

Tables 2 and 3 give the results so far obtained for pressure and temperature for most of the flights examined; they are divided into three parts according to the direction of the flights when observed. (No easterly flights were recorded.) Where flights were recorded as south-west or north-west one half has been credited to each direction. Tables 6 and 7, in the next section, show wind speed and direction at starting points.

Table 2. *Barometric pressure at supposed origin of flights*, 1933–6

Barometer		Rising	Falling	Little change
Flight direction	North	14	10	1½
	West	8	1	1½
	South	11	1	3
	Total	33	12	6

Table 3. *Temperature at supposed origin of flights*

Thermometer		Rising	Falling	Little change
Flight direction	North	8½	3	13
	West	4	3	3½
	South	8½	1	3½
	Total	21	7	20

Taken together, these tables seem to show a distinct tendency for flights to occur during or after periods of light to moderate winds, with rising barometer and rising or steady temperature. Such conditions are usually associated with anticyclonic weather; they are most favourable for crossing the sea, and are likely to improve rather than to deteriorate.

Although reached by a process not far removed from guesswork, the results are consistent enough to suggest that they are not far wide of the truth. It will be noticed that the effect of weather conditions is most strongly marked in the case of the southerly flights. This is to be expected, since there is much less doubt of the starting points in these cases; most of the southerly flights probably started quite close to the places where they were observed, while many of the northerly flights may have originated in districts far inland from the nearest points across the Channel which were used as a basis for the tables.

5. THE EFFECT OF WIND ON MIGRATION

It has often been supposed that all the so-called migrations of Lepidoptera are involuntary, and that they are due to the insects being helplessly blown along by the wind. If this were so, we should expect migrations to occur in more boisterous conditions than those described above, and in particular to take place in periods of strong winds rather than in calms. We should also expect the direction of flight always to agree with that of the wind, both at the starting point of the migration and wherever the flights were later observed.

In many of the available records, not only is the direction of the wind at the time of observation recorded, but also its strength in Beaufort numbers or their equivalent. These numbers were devised by Admiral Beaufort to allow winds to be divided into classes according to strength estimated by various means, and are used by sailors and meteorologists. The numbers are placed in the first row of the following tables, and their equivalent in miles per hour is recorded beneath each one. Table 4 shows the various strengths of winds in which migrations in different directions have been seen passing; Table 5 gives the same data, but shows whether the flight was in each case with, against, or across the wind. The column corresponding to Force 0, or Calm, has been left out of the second table as it is of course impossible to say that moths fly with or against a calm. Another discrepancy between the two tables is accounted for by the fact that some records state that flights took place in winds of variable direction, giving the strength but not the compass points; these could be included in the first table but not in the second. They are well worth notice, since the fact that a flight has taken place in a wind of, say, Force 3, which varied in direction without affecting the direction of the flight, is in itself a repudiation of the theory that migration is wholly due to the action of wind.

One of the most remarkable records of this kind reports a migration of hundreds of *P. gamma* to the north in the Scilly Isles in 1936. The flight continued for eight days, although the wind blew sometimes against the line of flight and sometimes across it, and varied in strength from a light breeze to Force 5 (19–24 m.p.h.) or even higher. It is unlikely, however, that the moths allowed themselves to be exposed to the full force of this wind for more than a few seconds at a time; observations made on other occasions show that when

these and other Lepidoptera are flying in a strong wind they tend to keep low among the herbage, and to take advantage of any cover they can find.

When flights are described as taking place partly with and partly across the wind (i.e. a flight to the north in a south-west wind), one half has been credited to each column. This has also been done when the strength of the wind is given as between two Beaufort numbers, for example, "Wind S. Force 2–3". It has sometimes been necessary to divide a flight into quarters on the same principle.

Table 4. *Wind force at place of observation of flights*, 1933–7

Beaufort numbers = miles per hour		0 Calm	1 1–3	2 4–7	3 8–12	4 13–18	5 19–24
Flight direction	North	6½	3½	6½	5	1½	2
	West	1	3	4	1	.	.
	South	2	8	3	2	½	½
	Total	9½	14½	13½	8	2	2½

Table 5. *Relationship between flight and wind direction at various wind speeds, at place of observation*, 1933–7

Beaufort numbers = miles per hour	1 1–3	2 4–7	3 8–12	4 13–18	5 19–24	Total
Flight with wind	4	3	2½	.	.	9½
Flight against wind	4	4	3½	½	.	12
Flight across wind	5½	6½	2	1½	2½	18

Table 4 shows that, although flights are more numerous in light winds, nearly a quarter of the flights were observed in winds of Force 3 or over, and that more than one flight occurred in a wind of Force 5, i.e. a "Fresh Breeze", 19–24 miles per hour. Should wind be the important factor in migration, then flights at the higher speeds should be with the wind; flights against the wind, if they took place at all, should occur only in the gentle winds. Table 5 shows that this is not the case and that there are actually more flights against the wind than with it. The largest number of flights are those across the wind; this is natural, since two directions are included in the expression "across". If this figure is divided into two, to allow for this, it will be seen that there is practically no effect of wind at all; the preponderance of flights against, over flights with the wind is so small as not to be significant. The lower right-hand diagram on Fig. 5 illustrates the effect of wind in diagrammatic form. Here, all winds are reduced to one direction, and the angle of flight to that direction is calculated. No allowance is made for wind speed, but by arranging darts on the logarithmic system used in Fig. 7 some indication of the numbers of insects involved is given, as apart from the number of flights.

Tables 6 and 7 give the data for presumed starting points of the migrations, and the results are comparable to those shown in Tables 4 and 5. There is a tendency for the wind to be stronger at the presumed starting point than at the place of observation, and for more flights to be across the wind than with or against it, but the differences are small, and probably not significant.

Table 6. *Wind force at presumed starting place of flights*, 1933–6

Beaufort numbers = miles per hour ...	0 Calm	1 1–3	2 4–7	3 8–12	4 13–18	5 19–24
North	6	3	6	5	2½	3
West	.	1½	3	5	½	.
South	3½	4	3	2	1	2
Total	9½	8½	12	12	4	5

Table 7. *Relationship between flight and wind direction at various wind speeds, at presumed starting place*, 1933–6

Beaufort numbers = miles per hour ...	1 1–3	2 4–7	3 8–12	4 13–18	5 19–24	Total
Flight with wind	2	2	2¼	½	½	7¼
Flight against wind	1½	2¼	3	1	¾	8½
Flight across wind	4½	6¾	6¾	2½	3½	24

6. SUMMARY

1. Records of the presence and movements in Great Britain of the moth *Plusia gamma* L. from 1932 to 1937 have been collected from amateur Lepidopterists and others by the Insect Immigration Committee of the South-Eastern Union of Scientific Societies. The moths have been seen in varying numbers in each of these years, and an account of their distribution in each year is given. Only two winter records have been received, although such records were specially asked for. Both these concerned pupae.

2. About fifty records give the direction of flight of the moths. From these it is shown that there is a general tendency for northward movements to preponderate in spring, and southward movements in autumn. Westward immigration from across the North Sea seems to occur regularly in mid-August.

3. A study of records in which direction and strength of wind are given show that wind direction has little or no effect on the direction of migratory flights, and that migrations can take place in adverse winds of Force 4 (13–18 m.p.h.) or in cross winds of Force 5 (19–24 m.p.h.).

4. Possible starting points of migrations have been chosen by prolonging the line of flight backwards from the point of observation to the nearest point on the Continent, and weather conditions for the period immediately preceding the flights have been studied. There appears to be a tendency for migrations to begin in periods of rising barometer, rising or steady temperature, and light or moderate winds. Wind direction at presumed starting points seems to have no influence on the direction of migration.

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BIRD AND ANIMAL ACTIVITY IN THE ARCTIC

By A. J. MARSHALL

In the past, almost without exception, zoologists have reported constant activity among birds and other animals in the perpetual light of the arctic summer. This is possibly accounted for by the extreme vigilance of all tundra species, coupled with the open nature of the country which renders the human observer visible at great distances. These arctic animals, naturally, are exceptionally alert, because of the open nature of their habitat. They have usually vacated their nesting or resting places and are very active indeed long before they are seen by the observer.

During a recent summer expedition to West Spitsbergen (Svalbard) attention was paid to the question of perpetual activity. Certain species of birds, notably the tern (*Sterna macrura*), the eider duck (*Somateria mollissima*), the skua (*Stercorarius parasiticus*) and possibly the purple sandpiper (*Calidris maritima*) undergo a distinct period of quiescence. At Klaas Billen Bay, in the "Inner Fjord Zone" (Summerhayes, V. S. & Elton, C. S. (1928), *J. Ecol.* 16: 256) this period appeared to extend for a couple of hours after 1 a.m. each day. It coincides roughly with the time during which the sunlight, temperature, and wind velocity are at a minimum. (For this information I am indebted to Prof. H. Tollner of the Zentralanstalt für Meteorologie, Vienna, a co-worker on our expedition.)

On one species only could satisfactory observation be made. This was the arctic tern, which had established an extensive ternery on the shingle about the huts in which we lived. These birds were in residence before we arrived, and after the first few hours we were subjected to a vicious attack by them every time we left the huts. They unmercifully persecuted the fulmar petrels and gulls which flew over the ternery from time to time, and no robbing skua dared approach their colony. During the quiescent period however, when the sitting tern slept on the eggs and its mate fitfully dozed a few yards away, passing kittiwakes (*Rissa tridactyla*) and fulmars (*Fulmarus glacialis*) and even the hereditary enemy the skua were allowed to fly over low without molestation. Despite the fact that the sitting bird was sleeping, the non-sitting bird never slept for more than a few minutes at a time. Time and again it would suddenly untuck its head and gaze suspiciously around, often making a short flight as if to satisfy itself that all was well. A human figure appearing half a mile away over the barren tundra would provoke the whole colony into noisy

activity. Had hiding facilities within the ternery not been available I would never have guessed that a period of comparative inactivity existed. And it is probable that a similar period occurs with many other species as well.

In the recently described glacial feeding zone (Hartley, C. H. & Fisher, J. (1936), *J. Anim. Ecol.* 5: 370) at the head of Klaas Billen Bay, there appeared to be, as Hartley and Fisher suggest, little evidence of any great numerical fluctuation in the constant stream of kittiwakes which flew to and fro along the coast and over the tundra. A few kittiwakes would doze after feeding, basking in the sunlight on the ice-smoothed boulders carried down to the bay by the nearby glacier. The vast majority, however, would return down fjord to their colonies. Contrary to Fisher and Hartley, we found (in 1937) fulmars far more numerous than kittiwakes in the feeding zone. For 24 hr. the fulmar flock fed with the kittiwakes at the mouths of the ice streams which poured from under the ice cliffs at the face of the glacier; individuals gradually falling away from the whirling, dipping mass to rest replete, dozing and preening on the water among the drifting ice-blocks. At about 6 a.m. the resting fulmar flock appeared to decrease in numbers, and during the day there were never so many birds resting on the water as during the "night" hours after 9 or 10 p.m. The birds were breeding in cliffs a couple of miles away. The stomachs of both species contained a great number of crustaceans.

In many other species I could detect no distinct rest period whatever. In the colonial cliff nesting species of little auks (*Alle alle*), puffins (*Fratercula arctica*) and guillemots (*Uria lomvia*) which we observed at Sudgat in the north-west of the island, I could find no slack period in either flight or fishing. For the whole of 24 hr. birds flew around the cliffs in great flocks, or otherwise exhibited constant activity: feeding, fishing or engaging in the curious noisy communal gatherings which one sometimes observes on the feeding waters. (Little auk: Montague, F. A. (1926), *Ibis*: 151; guillemot: Longstaff, T. G. (1924), *Ibis*: 493.)

At all times it was strikingly apparent that local weather conditions are a big factor in controlling activity. Unusually heavy winds, strong sunlight (and the rare period of excessive rain) always modified activity. The icy glacial winds sweeping over the tundra would force birds to take advantage of any scanty cover offered. A fine burst of sun would interrupt their feeding; and sandpipers, terns, gulls, snow-buntings and other birds perching fluffed in the pale sunlight would not be an unfamiliar sight.

Among the few mammals observed, the arctic fox (*Alopex lagopus*) and the ring seal (*Phoca hispida*) were noted at all times: the fox out foraging, the seal swimming, or basking on the floating bergs. I was unable to arrive at any definite conclusion about the activity of these mammals.

Summary

1. The arctic tern (*Sterna macrura*) and possibly other species, have periods of quiescence in the perpetual arctic light; and these periods may be correlated with meteorological conditions.

2. In many species, such as the fulmar petrel (*Fulmarus glacialis*), there is no apparent period of inactivity: it is possible that these rest only when replete or tired.

3. Local weather conditions (such as sudden sunlight or icy winds) may abruptly provoke inactivity.

THE FOOD OF PARTRIDGE CHICKS (*PERDIX PERDIX*) IN GREAT BRITAIN

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(*With 2 Figures in the Text*)

1. Introduction

The work on which this paper is based forms part of a research into the ecology of game birds carried on by the Bureau of Animal Population. This research has been financed by a grant from Imperial Chemical Industries and by the donations of landowners and shooting men. We wish to thank all those who have helped in this way, and also by sending us specimens for examination.

We are indebted to E. Arthurs, Department of Botany, Oxford, for identification of some of the seeds; to E. W. Aubrook, Hope Department of Entomology, Oxford, who identified the Coleoptera; and to Dr K. G. Blair of the British Museum (Natural History) for a note on the *Phytonomus* larvae. We have also to thank Prof. G. D. Hale Carpenter who allowed us the facilities of the Hope Department of Entomology at Oxford for the entomological work.

2. Material and technique

The crop contents of sixty-nine partridge chicks, received between 1934 and 1937 from various estates in Britain, have been analysed. As it is extremely difficult to obtain young partridges for crop examination, our only source of material was through accidental deaths. Actually, the majority of the birds we examined were killed by mowing machines cutting hay, clover, lucerne, etc., in which the young birds were living. Our sample is not, therefore, truly representative of the whole population. Probably more young partridges live in growing corn crops than in grass and clover, but there was no means of obtaining specimens from corn crops in June and July, during the first 6 weeks of the partridge's life. This fact naturally limits the invertebrate fauna available to the birds we examined, especially those under about 2 weeks of age. The older chicks, being able to fly from one field to another, probably took a more random sample of the food available in both green and corn crops.

The contents of each crop, mainly insect material, were stored in alcohol until time for sorting. The process of sorting was as follows. All vegetable

material was separated out and treated as described in a previous paper (**1**). The insects and other animals were then sorted into orders and kept in separate tubes of alcohol, except for the beetles and some bugs which were dried and mounted for identification. The numbers of individuals of each species or group of species were recorded on separate cards for each crop. These cards are preserved in the Bureau of Animal Population.

Before determining the volumes of the various constituents, the crops were arranged in four age classes: from hatching until 7 days, from 8 to 14, from 15 to 21 and over 21 days. When the age of a chick was not known from the

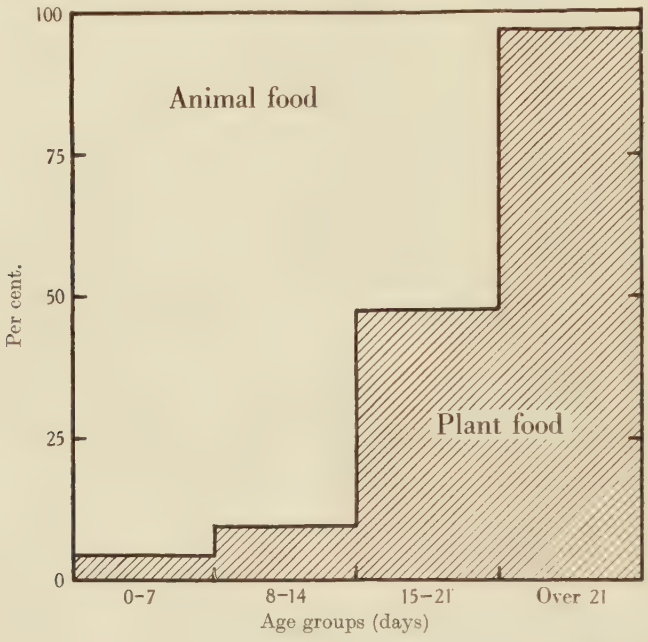

Fig. 1. Proportions by volume of animal and plant foods in partridge chick crops.

original data, this was estimated from its weight by use of the weight/age curve shown in Fig. 2. This curve has been compiled from data obtained from hand-reared chicks of known age (Table 1).

In the determination of volumes, insects, etc., of the same species, or group of species, were combined in each age class; excess alcohol was removed with blotting paper, and the volume determined by displacement in a measuring tube containing alcohol. Species which had been dried for identification were first boiled for 5 min. to expel enclosed air and remove them from the mounting cards; the water was then poured off and they were washed with cold alcohol. They were then measured volumetrically as above. The boiling treatment is necessary, as without it the dried insects will float in the measuring tube.

Table 1. *Weights of partridges at different ages*

Age in days	Average weights in grams of four groups of partridges reared (*a*)	(*b*)	(*c*)	(*d*)
1	10·0	—	—	—
2	9·3	—	—	—
3	9·1	—	—	—
4	10·6	—	—	—
5	12·1	—	—	—
6	12·9	14·9	—	—
7	—	—	18·8	18·4
8	16·4	—	—	—
9	18·5	—	—	—
11	23·0	—	—	—
12	25·4	—	—	—
13	27·3	28·0	—	—
14	28·3	—	27·0	35·4
15	32·2	—	—	—
16	33·1	—	—	—
17	35·1	—	—	—
18	38·8	—	—	—
19	40·3	—	—	—
20	41·5	44·5	—	—
22	46·1	—	43·5	—
23	50·7	—	—	—
27	—	68·0	—	—
28	—	—	68·5	—
34	—	94·5	—	—
35	—	—	101·4	—
42	—	—	130·3	—

3. Results of crop analysis

(*a*) *Animal food.* Table 2 gives the species or groups of species of insects and other animals identified in all crops, together with the numbers of each obtained in each age class. Where a species occurred in more than one crop the frequency is given in brackets.

In many instances the specimens were too mangled for complete identification, especially Diptera and nymphs of Heteroptera. In some cases, especially the Aphididae, where the naming of species would have involved seeking the co-operation of specialists, we have been content with names of orders or families. The parasitic Hymenoptera, various arachnids and the larvae of Lepidoptera, which also were not fully identified, comprised a large number of species, no one of which had any importance numerically. Altogether 143 identifications are listed, though the actual total of species is probably in the neighbourhood of 200.

Tables 3–6 summarize the individual crop analyses in the four age classes. Each crop is given a reference number for the locality from which it was obtained. The following is a list of these localities, with the numbers pertaining to them:

Hampshire. Tichborne, 1, 2; Sutton Scotney, 19, 20, 21, 25, 26, 39, 53; Alresford, 41; Red Rice, 52; Lymington, 58. Isle of Wight. Bowcombe, 42, 50, 51. Sussex. Amberley, 22, 23. Berkshire. Ilsley, 32, 33, 34, 46, 55;

Table 2. *Animal species identified, with abundance and frequency in each age class*

	1st week	2nd week	3rd week	Over 3 weeks	Total
INSECTA					
COLLEMBOLA					
Sminthurus viridis L.	556 (18)	611 (15)	64 (5)	—	1231
?*Orchesella* sp.	1	9 (3)			10
ORTHOPTERA					
Blattidae					
Ectobius panzeri Steph.	—	—	—	2	2
Acrididae (spp. indet. nymphs)	7 (3)	18 (3)	1	1	27
DERMAPTERA					
Forficula auricularia L.	29 (6)	4 (2)	3 (3)	2	38
HEMIPTERA-HETEROPTERA					
Coreidae (sp. indet.)	—	4	—	—	4
Lygaeidae (spp. indet.)	1	—	11	—	12
Reduviidae					
Nabis sp.	—	4	1	—	5
Anthocoridae					
?*Anthocoris* sp.	—	—	2	—	2
Capsidae					
Lygus sp.	—	—	1		1
Spp. indet.	8	103 (4)	35	—	146
Other Heteroptera indet.	10 (4)	21 (3)	4	—	35
HEMIPTERA-HOMOPTERA					
Delphacidae					
Delphacinus mesomelas Boh.	1	—	—	—	1
?*Delphacinus* sp.	—	—	1		1
Cercopidae					
Philaenus spumarius L.	1	3 (2)	5		9
Philaenus campestris Fall.	—	4	—	—	4
Philaenus sp. nymphs	—	2 (2)	1		3
Jassidae					
Acocephalus albifrons L.	2	2	1	—	5
Acocephalus bifasciatus L.	—	1	—		1
Acocephalus nervosus Schrk.	—	—	1		1
Acocephalus spp. nymphs	28 (7)	23 (6)	57 (3)	1	109
Eupelix cuspidata Fab.	—	—	8	—	8
Athysanus obscurellus Kbm.	—	—	1		1
Athysanus sp.	—	—	2	—	2
Deltocephalus pascuellus Fall.	—	13	—	—	13
Deltocephalus ocellaris Fall.	—	—	5	—	5
Deltocephalus pulicaris Fall.	—	3 (3)	—		3
Deltocephalus socialis Flor.	4 (2)	4	2	—	10
Deltocephalus sp. nymphs	11 (4)	3 (2)	15 (4)	5	34
Limotettix 4-*notata* Fab.	5	9 (2)	—		14
Limotettix ?*sulphurella* Zett.	—	—	10		10
?*Limotettix* sp.	1	3 (2)	—	—	4
Cicadula sexnotata Fall.	4	1	—	—	5
Cicadula sp.	—	1	—	—	1
Spp. indet. nymphs	32 (7)	23 (8)	10 (3)		65
Aphididae (spp. indet.)	468 (17)	251 (11)	23 (3)	4 (2)	746
Aleyrodidae (spp. indet.)	—	8	45	—	53
NEUROPTERA					
Chrysopidae					
?*Chrysopa* sp.	—	—	—	1	1
LEPIDOPTERA					
Imagines, spp. indet.	3	10	19 (3)	1	33
Larvae, spp. indet.	60 (15)	24 (11)	17 (6)	2 (2)	103
COLEOPTERA					
Staphylinidae					
Tachyporus hypnorum F.	1	7 (3)	4 (3)	—	12
Tachyporus chrysomelinus L.	1	2 (2)	—	—	3
Tachyporus sp.	—	—	1	—	1
Tachinus sp.	—	1	-	-	1

Table 2 (*cont.*)

	1st week	2nd week	3rd week	Over 3 weeks	Total
COLEOPTERA (*cont.*)					
Staphylinidae					
Astilbus canaliculatus F.	2	—			2
Xantholinus linearis Ol.	—	—	1		1
Philonthus varius Gyll.	—	2 (2)	—	—	2
Oxytelus sp.	—	1	—	—	1
Stenus similis Hbst.	—	—	2		2
Hypocyptus longicornis Pk.	—	1	—	—	1
Curculionidae (Weevils)					
Phyllobius viridiaeris Laich.	32 (3)	137 (2)	—		169
Phyllobius parvulus Ol.	—	2	—		2
Sitona sulcifrons Thunb.	1	1	3 (2)	—	5
Sitona humeralis Steph.	—	2	1		3
Sitona puncticollis Steph.	10 (4)	52 (5)	9 (2)	1	72
Sitona lineatus L.	1	—	1	—	2
Sitona hispidulus F.	—	7 (5)	—		7
Sitona flavescens Marsh.	—	1	—		1
Sitona crinitus Hbst.		—	—	1	1
Sitona sp.	1	1	—	1	3
Apion assimile Kirb.	5	1	4 (2)		10
Apion aestivum Germ.	1	—	9 (3)		10
Apion curtirostre Germ.	1	1	—		2
Apion flavipes Pk.	—	1	1	—	2
Apion pisi F.		—	—	2	2
Apion loti Kirb.		—	1		1
Apion apricans Hbst.	—	—	1	—	1
Apion sp.	1	2 (2)	—	—	3
Phytonomus nigrirostris F.	7 (3)	3 (3)	1	—	11
Phytonomus punctatus F.	—	1	—		1
Phytonomus trilineatus Marsh.	—	—	1		1
Phytonomus sp.	—	1	1	—	2
Phytonomus larvae	501 (14)	222 (9)	114 (4)		837
Miccotrogus picirostris F.	2 (2)	—	—		2
Rhinoncus pericarpius L.	—	—	1		1
Gymnetron sp.	—	—	1	—	1
Amalus haemorrhous Hbst.		—	—	1	1
Liosoma deflexum Pz.	—	1	—		1
Philopedon plagiatus Schol.	—	—	—	2	2
Stenocarus fuliginosus Marsh.	—	—	—	1	1
Carabidae					
Bembidion lampros Hbst.	1	1	—		2
Pterostichus madidus F.	—	—	1		1
Pterostichus sp.	—	—	1		1
Metabletus obscuroguttatus Duft.	—	—	1	—	1
Amara communis Pz.	—	—	1	—	1
Demetrius atricapillus L.	1	—			1
Trechus quadristriatus Schr.	—	7 (2)			7
Harpalus aeneus F.	—	—		1	1
Anchomenus dorsalis Pont.	—	—		1	1
Chrysomelidae					
Chaetocnema concinna Marsh.	—	—	—	2	2
Phyllotreta nodicornis Marsh.	—	—	—	1	1
Phyllotreta vittula Redt.	—	—	—	1	1
Crepidodera ferruginea Scop.	—	1	—		1
Longitarsus sp.	—	—	1		1
Cantharidae					
Cantharis fulvicollis F.	—	1		—	1
Cantharis lateralis L.	—	3	—	—	3
Malachius viridis F.	—	1	—	—	1
Elateridae					
Agriotes lineatus L.	—	2 (2)	2 (2)		4
Agriotes sputator L.	—	3 (3)	1		4
Agriotes obscurus L.	—	4 (3)	1	—	5
Athous longicollis Ol.	—	—	1		1
Adrastus nitidulus Marsh.	—	—	—	1	1
Byrrhidae					
Simplocaria semistriata Ill.	—	2	—	—	2

Table 2 (*cont.*)

	1st week	2nd week	3rd week	Over 3 weeks	Total
COLEOPTERA (*cont.*)					
Cholevidae					
Ptomophagus subvillosus Goez.	1	—	—	—	1
Lathridiidae					
Enicmus transversus Ol.	1	—	—	—	1
Coccinellidae					
Micraspis 16-*punctata* L.	—	—	1	—	1
Nitidulidae					
Meligethes viridescens F.	—	—	—	15	15
HYMENOPTERA					
Tenthredinoidea					
Cephus pygmaeus L.	1	—		—	1
Rhogogaster viridis L.	—	1		—	1
Ichneumonoidea (spp. indet.)	5 (3)	12 (3)	3 (3)	1	21
Proctotrypoidea (spp. indet.)	3 (3)	4 (2)	—	1	8
Chalcidoidea (spp. indet.)	6 (5)	3 (3)	1		10
Cynipoidea (sp. indet.)	1	—	—		1
Formicoidea (Ants)					
Myrmica scabrinodis Nyl.	—	8 (2)	—	-	8
Acanthomyops flavus F.	—	73 (4)	522 (3)	—	595
Acanthomyops niger L.	9 (4)	17 (5)	2	12 (4)	40
Cocoons	—	258 (3)	1625 (4)	-	1883
Larvae	—	23	—	—	23
Other Hymenoptera indet.	4 (3)	4 (3)	8 (5)	—	16
DIPTERA (Flies)					
Tipulidae					
Tipula spp.	2 (2)	1	—	—	3
Limnobius sp.	1	—	—	-	1
Asilidae					
Leptogaster cylindrica Deg.	—	1	—	-	1
Empidae					
Hilara sp.	—	1	—	.	1
Dolichopodidae (spp. indet.)	—	2	—	—	2
Phoridae (spp. indet.)	1	1	-	-	2
Pipunculidae					
Pipunculus sp.	—	1	—	—	1
Trypaneidae					
Ditricha guttularis Meig.	—	1	—	—	1
?Sapromyzidae (spp. indet.)	—	2 (2)	—	-	2
Agromyzidae (spp. indet.)	1	1	—	—	2
Ephydridae					
Hydrina sexmaculata Becker	—	1	—	—	1
Chloropidae					
Meromyza variegata Meig.	—	—	1	—	1
Meromyza sp.	1	4 (2)	1	—	6
Spp. indet.	5 (3)	6	4 (2)	5 (3)	20
Tachinidae (sp. indet.)	—	—	—	1	1
Muscidae (spp. indet.)	1	1	—	—	2
Other Diptera indet.	4 (3)	2 (2)	-	1	7
INSECTS INDETERMINABLE					
Imagines	11 (6)	1	—	3 (2)	15
Larvae	12 (7)	24 (9)	3 (2)	5 (5)	44
ARACHNIDA					
Acarina (Mites) (spp. indet.)	—	7	13	—	20
Araneida (Spiders) (spp. indet.)	49 (12)	38 (11)	56 (9)	6 (4)	149
Phalangida (Harvestmen) (spp. indet.)	23 (4)	8 (3)	17 (2)	—	48
CRUSTACEA, ISOPODA (Woodlice)					
Philoscia sp.	—	1	–	–	1
Armadillidium vulgare Latr.	—	—	1	—	1
MYRIAPODA, CHILOPODA (Centipedes)					
?Notophilidae (sp. indet.)	—	—	—	2	2
MOLLUSCA					
GASTROPODA (Snails) (spp. indet.)	—	1	2 (2)	—	3

Table 3. *Individual crop analyses. 0–7 days*

Crop No.	Date	*Sminthurus viridis*	*Forficula auricularia*	*Acocephalus* spp.	Other Homoptera	Aphididae	Heteroptera	*Sitona puncticollis*	Other Curculionidae	Other Coleoptera	*Phytonomus* larvae	Lepidoptera larvae	*Acanthomyops niger*	Other Hymenoptera	Diptera	Other adult insects	Other larval insects	Araneida	Phalangida	Total animals	Seeds	Green leaves
1	16 June 1934	47	.	.	2	35	1	.	.	.	.	5	.	2	.	1	.	.	1	94	.	.
2	16 June 1934	31	.	.	.	57	.	.	.	.	.	6	.	1	.	.	.	.	.	95	.	.
3	26 June 1934	8	.	.	3	.	8	.	5	.	.	.	.	2	1	.	1	3	.	31	.	.
4	24 June 1935	.	.	3	9	2	.	.	14	.	73	4	.	1	2	4	.	.	.	112	.	.
5	24 June 1935	5	.	2	8	.	.	.	15	.	98	3	.	.	2	3	.	1	.	137	.	.
6	24 June 1935	.	.	.	2	.	.	.	.	.	57	3	.	1	3	1	1	.	.	68	.	.
7	4 July 1934	129	.	.	8	.	.	.	2	.	.	14	.	6	3	7	.	16	.	193	.	.
8	28 June 1935	18	9	2	.	13	8	.	2	1	24	5	.	1	1	2	1	2	.	77	.	.
9	28 June 1935	4	10	.	.	2	.	2	.	.	.	.	.	1	.	.	.	.	.	22	.	.
10	28 June 1935	116	6	2	2	6	.	.	.	4	1	2	.	2	.	.	4	7	.	152	.	.
11	28 June 1935	13	2	1	.	1	.	.	.	.	.	1	.	.	.	.	.	5	.	23	.	.
12	28 June 1935	40	.	.	.	3	.	1	.	.	.	.	.	.	.	.	3	2	.	57	.	.
13	22 June 1936	1	.	.	1	28	.	.	.	.	29	8	1	.	.	.	.	.	.	60	.	.
14	22 June 1936	.	.	.	.	41	.	.	.	.	18	.	.	.	.	.	.	.	.	59	.	.
15	25 June 1936	8	1	8	.	22	1	.	5	1	36	.	4	2	1	2	.	3	.	94	.	.
16	25 June 1936	2	1	.	3	17	.	.	.	.	98	1	.	.	.	.	.	3	.	125	.	.
17	25 June 1936	7	.	5	.	18	1	.	1	.	20	1	1	.	1	.	1	1	.	57	+	.
18	25 June 1936	15	.	.	19	24	.	.	1	1	21	1	3	.	1	.	.	1	.	87	.	.
19	26 June 1936	15	.	.	1	65	.	.	3	1	5	1	.	1	.	2	1	.	6	99	.	+
20	26 June 1936	21	.	.	1	45	.	6	1	.	9	5	.	.	.	.	.	5	8	100	+	+
21	26 June 1936	76	.	7	.	89	.	.	3	.	12	1	.	.	.	.	.	5	8	201	.	.
	Totals	556	29	30	59	468	19	10	52	8	501	60	9	20	16	22	12	49	23	1943		

Table 4. *Individual crop analyses.* 8–14 *days*

Crop No.	Date	*Smithurus viridis*	*Forficula auricularia*	Acrididae nymphs	*Acocephalus* spp.	Other Homoptera	Aphididae and Aleyrodidae	Heteroptera	*Sitona puncticollis*	*Phyllobius viridiaeris*	Other Curculionidae	Other Coleoptera	*Phytonomus* larvae	Lepidoptera larvae	Formicoidea	Formicoidea cocoons + larvae	Other adult Hymenoptera	Diptera	Other adult insects	Other larval insects	Arancida	Phalangida	Other animals	Total animals	Seeds	Green leaves
22	22 June 1934	1	.	8	.	2	.	.	.	.	.	1	.	7	23	144	.	.	.	2	3	.	.	191	+	.
23	22 June 1934	2	.	8	.	.	1	6	.	.	1	.	1	3	34	96	.	2	.	.	1	.	.	155	.	+
24	2 July 1935	113	2	.	2	.	1	.	.	.	4	3	.	.	.	.	.	2	1	.	3	.	7	138	+	.
25	20 June 1934	3	.	.	.	5	5	5	.	2	1	1	.	4	18	41	.	1	.	.	.	.	.	86	.	.
26	20 June 1934	3	.	.	2	9	3	1	.	.	.	.	.	1	1	.	.	.	.	1	3	.	.	24	+	.
27	2 July 1936	62	.	.	.	1	3	.	7	.	2	2	13	1	.	.	1	.	.	2	.	.	.	94	+	.
28	2 July 1936	128	.	.	.	3	3	.	16	.	4	13	21	1	.	.	.	.	6	2	6	.	.	203	+	.
29	2 July 1936	107	.	.	.	3	.	.	14	.	4	8	35	1	.	.	.	1	1	5	5	.	.	183	+	.
30	26 June 1936	1	.	.	.	3	9	.	.	.	.	.	16	.	.	.	1	1	1	1	2	1	.	36	.	+
31	27 June 1936	1	.	.	.	1	13	.	.	.	1	.	12	.	.	.	.	.	.	.	.	.	.	28	+	.
32	10 July 1934	.	.	.	8	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	16	+	.
33	10 July 1934	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	21	+	.
34	10 July 1934	3	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	7	+	.
35	27 June 1934	62	.	2	3	30	.	100	.	135	.	3	66	.	17	.	12	13	10	3	6	.	.	462	.	.
36	9 July 1935	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	23	.	.
37	9 July 1935	.	.	.	6	1	.	.	10	.	.	2	.	3	.	.	3	2	2	5	.	.	.	34	.	.
38	9 July 1935	28	.	.	1	.	4	.	5	.	.	4	.	1	.	.	.	.	.	.	3	.	.	46	+	.
39	22 June 1934	78	.	.	.	7	216	20	.	.	4	.	44	1	4	.	7	3	.	3	2	.	1	390	.	.
40	5 July 1935	.	2	.	4	.	.	.	.	.	3	2	14	.	1	.	.	.	.	.	.	.	1	27	.	.
	Totals	611	4	18	26	69	259	132	52	137	25	39	222	24	98	281	24	25	20	24	38	8	9	2145		

Table 5. *Individual crop analyses.* 15–21 *days*

Crop No.	Date	*Sminthurus viridis*	*Forficula auricularia*	Acridiidae nymphs	*Acocephalus* spp.	Other Homoptera	Aphididae and Aleyrodidae	Heteroptera	*Sitona puncticollis*	Other Curculionidae	Other Coleoptera	*Phytonomus* larvae	Lepidoptera imagines	Lepidoptera larvae	Formicoidea	Formicoidea cocoons	Other adult Hymenoptera	Diptera	Other larval insects	Araneida	Phalangida	Other animals	Indet. animal fragments	Total animals	Seeds	Green leaves	Flowers
41	8 July 1935	2	.	1	.	6	.	4	.	2	4	1	10	7	.	2	3	.	.	11	.	.	+	50	+	+	.
42	1 July 1936	.	.	.	1	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.
43	4 July 1934	.	1	.	38	1	.	1	.	4	2	.	.	1	.	.	.	.	2	2	.	.	+	51	+	.	.
44	4 July 1934	.	1	.	18	21	.	.	.	.	1	.	.	5	.	.	1	.	.	.	.	.	+	34	+	.	.
45	21 July 1936	.	.	.	.	21	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	+	24	+	+	.
46	20 July 1935	10	.	.	.	.	.	.	.	2	1	.	4	.	6	1	.	.	.	9	.	.	+	33	+	+	.
47	20 July 1934	13	.	.	.	20	45	37	.	1	.	.	5	.	194	29	3	4	.	9	.	.	+	360	+	.	.
48	3 July 1936	1	.	.	.	.	.	.	2	.	5	.	.	1	.	.	.	.	.	3	.	.	+	12	+	.	.
49	3 July 1936	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	3	+	.	.
50	25 June 1934	.	.	.	.	.	10	.	.	2	1	27	.	.	.	.	2	.	.	1	.	1	.	44	+	.	.
51	25 June 1934	.	.	.	.	.	10	.	7	14	2	84	.	.	.	.	2	.	1	4	2	1	.	128	+	.	.
52	11 July 1935	38	1	.	.	1	.	.	.	.	1	2	.	.	324	1593	.	1	.	.	.	.	.	1961	+	.	.
53	17 Oct. 1934	.	.	.	1	2	3	12	.	1	1	.	.	1	.	.	1	1	.	15	15	13	.	66	.	.	.
54	5 July 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.
55	6 July 1934	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Totals	64	3	1	59	60	68	54	9	26	19	114	19	17	524	1625	12	6	3	56	17	16		2772			

Table 6. *Individual crop analyses. Over* 21 *days*

Crop No.	Date	Orthoptera	*Forficula auricularia*	Hemiptera	Curculionidae	Other Coleoptera	Lepidoptera larvae	Formicoidea	Other adult Hymenoptera	Diptera	Other adult insects	Other larval insects	Araneida	Chilopoda	Indet. animal fragments	Total animals	Seeds	Green leaves	Flowers
56	30 July 1934	.	.	5	.	.	.	2	1	3	1	1	.	.	.	13	+	+	.
57	16 July 1934	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.
58	5 Aug. 1934	2	2	.	.	.	.	.	.	.	1	1	1	.	.	7	+	.	.
59	1 Aug. 1934	.	.	2	.	2	1	2	1	3	2	1	3	2	.	19	+	+	.
60	1 Aug. 1934	.	.	.	.	.	.	.	.	1	1	.	1	.	.	3	+	.	.
61	1 Aug. 1934	.	.	.	.	.	1	.	.	.	.	1	.	.	.	2	+	+	.
62	16 July 1935	1	.	2	.	18	.	1	.	.	.	1	1	.	.	24	+	.	.
63	Aug. 1937	.	.	.	7	1	.	7	.	.	.	.	.	.	+	15	+	.	.
64	1937	.	.	.	2	1	.	.	.	.	.	.	.	.	.	3	+	+	.
65	2 Sept. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
66	2 Sept. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	–	.
67	2 Sept. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
68	2 Sept. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	–	.
69	2 Sept. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Totals	3	2	10	9	22	2	12	2	7	5	5	6	2		87			

Aston Tirrold, 24. Shropshire. Cressage, 27, 28, 29. Hertfordshire. Knebworth, 3, 4, 5, 6, 35, 47, 59, 60, 61. Norfolk. Sandringham, 8, 9, 10, 11, 12; Crown Point, 30, 31; Wroxham, 62; Thornham, 63, 64; Raveningham, 65, 66, 67, 68, 69; Castle Acre, 13, 14; Witchingham, 15, 16, 17, 18, 40, 54. Cambridgeshire. Six Mile Bottom, 56, 57. Lincolnshire. Denton, 43, 44. Yorkshire. Skelton, 37, 38. Northumberland. Longhirst, 7, 36. Perthshire. Elcho Park, 45. Forfarshire. Edzell, 48, 49.

The differences between the individual crop contents shown in these tables are attributable to three factors. Two of them, namely the differences in food available to chicks in various localities and the time of death in relation to the last emptying of the crop, do not require comment. A third factor is found in the opportunity a chick may have for making a large meal. This factor applies particularly to crops in which one item predominates. When a particular source of food is concentrated and does not need searching for, it is probable that the crop is filled to greater capacity than at any time when feeding is at random. This occurs in crop No. 35 which contained 135 adult weevils of the species *Phyllobius viridiaeris* and also in those crops of the second and third age classes containing large numbers of ants and their cocoons. Before, however, considering partridge chick feeding habits in general, it is necessary to consider other aspects of the food analysis.

The volumes of the various animal groups in each age class are given in Table 7 from which it is evident that the abundance of the different kinds of food given in Tables 3–6 is by no means a good index of their importance as diet. Nor, however, is the volume a reliable index, since a few large animals, only eaten rarely, may come to occupy a disproportionally large place in the

volume figures. In assessing the importance of different food items it is necessary to consider as well a third measure: the frequency of occurrence.

Table 7. *Volumes of insects, etc. (c.c.) eaten by partridge chicks*

	1st week	2nd week	3rd week	Over 3 weeks
Sminthurus viridis	0·25	0·30	0·03	
Acridiidae		0·45	0·02	
Forficula auricularia	0·45	0·10	0·10	
Homoptera (ex Aphids)	0·32	0·37	0·45	
Aphididae and Aleyrodidae	0·63	0·35	0·10	
Heteroptera	0·05	0·25	0·10	
Sitona puncticollis		0·45		
Phyllobius viridiaeris	0·40	0·80	0·10	0·10
Other Curculionidae		0·15		
Other Coleoptera	0·03	0·30	0·30	0·05
Phytonomus larvae	2·95	1·05	0·50	—
Lepidoptera: Imagines			0·30	
Larvae	1·45	0·70	1·20	
Formicoidea: Imagines	0·01	0·15	0·60	
Cocoons		1·20	1·75	
Other Hymenoptera, Imagines	0·05	0·10	0·04	
Diptera	0·05	0·05	0·01	
Other insects: Imagines	0·06	0·15	—	
Larvae	0·01	0·25	0·01	
Araneida	0·05	0·10	0·20	
Phalangida	0·15	0·05	0·40	
Other animals		0·05	0·15	0·20
Indet. animal fragments			0·15	0·10
Totals	6·91	7·37	6·51	0·45

Table 8. *Plant seeds, etc., eaten by partridge chicks in each age class, with their abundance, frequency and volume (c.c.)*

	Volume (c.c.)					Numbers			
Seeds	1st week	2nd week	3rd week	Over 3 weeks	Total volumes	1st week	2nd week	3rd week	Over 3 weeks
Ranunculus sp.	—	0·25	0·05	—	0·30	—	108	21 (3)	—
Silene inflata	—	—	+	0·50	0·50	—	—	2	274
Cerastium vulgatum	—	0·03	—	—	0·03	—	3	—	—
Stellaria media	—	+	0·08	0·57	0·65	—	2 (2)	22 (4	173
Caryophyllaceae (sp. indet.)	—	—	—	0·06	0·06	—	—	—	90 (2)
Myosotis arvensis	0·01	0·17	+	—	0·18	6	75	1	—
Calamintha acinos	0·05	—	—	—	0·05	1 fruit head	—	—	—
Polygonum sp.	—	0·01	+	0·04	0·05	—	1	1	5
Euphorbia exigua	—	—	—	0·01	0·01	—	—	3	7
Carex sp.	—	—	—	0·85	0·85	—	—	—	3400
Alopecurus agrestis	0·01	—	0·04	0·02	0·07	2	—	14 (2)	5 (2)
Avena sativa	—	—	—	0·03	0·03	—	—	—	1
Holcus lanatus	—	—	0·01	—	0·01	—	—	7	—
Hordeum sativum	—	—	—	4·14	4·14	—	—	—	108 (4)
Lolium perenne	—	0·02	—	0·21	0·23	—	8	—	103
Lolium italicum	—	0·09	0·19	—	0·28	—	64	132 (6)	—
Festuca pratensis	—	—	1·38	0·07	1·45	—	—	613	32
Dactylis glomerata	—	—	—	0·20	0·20	—	—	—	171
Poa pratensis	0·22	0·10	2·12	0·35	2·79	613 (4)	148 (4)	2425 (3)	648 (4)
Poa trivialis	—	—	0·30	—	0·30	—	—	983 (2)	—
Triticum sp.	—	—	—	4·15	4·15	—	—	—	112 (4)
Dari	—	—	0·03	—	0·03	—	—	1	—
Maize	—	—	0·20	—	0·20	—	—	12 bits	—
Sp. indet.	—	—	0·60	—	0·60	—	—	185	—
TOTAL VOLUME OF SEEDS	0·29	0·67	5·00	11·20	17·16	622	409	4422	5129
Green leaves and grass	0·05	0·09	0·28	0·95	1·37	(1)	(4)	(5)	(8)
Flowers and buds	—	—	0·03	0·33	0·96	—	—	(2)	(2)
Roots	—	—	—	0·90	0·90	—	—	—	(3)
TOTAL VOLUME OF VEGETABLE MATTER	0·34	0·76	5·91	13·38	20·39				

4. Evaluation of food items

It has been mentioned that to arrive at an estimate of the relative values, as food, of the various constituents of the crops, it is necessary to consider their abundance, volume and frequency of occurrence. This is the more necessary in the present case owing to the small number of crops available. Table 10 presents abundance and volume expressed, for comparison, as percentages, together with the frequency of occurrence of each group of animal species.

Table 10. *Percentage abundance and volume of insects, etc., in each age class, together with frequencies of occurrence*

Species or group of species	1st week			2nd week			3rd week		
	Abundance	Vol.	Frequency (21)	Abundance	Vol.	Frequency (19)	Abundance	Vol.	Frequency (15)
Sminthurus viridis	28·6	3·6	18	28·5	4·1	15	2·3	0·5	5
Acridiidae	—	—	—	0·8	6·1	3	0·1	0·3	1
Forficula auricularia	1·5	6·5	6	0·2	1·4	2	0·1	1·5	3
Homoptera	4·6	4·6	17	4·4	5·0	16	4·3	6·9	9
Aphididae	24·1	9·1	17	12·1	4·7	11	2·5	1·5	4
Heteroptera	1·0	0·7	5	6·2	3·4	5	1·9	1·5	4
Curculionidae	3·2	5·8	13	10·0	19·0	13	1·3	1·5	8
Other Coleoptera	0·05	0·4	5	1·8	4·1	10	0·7	4·6	10
Phytonomus larvae	25·8	42·7	14	10·3	14·3	9	4·1	7·7	4
Lepidoptera larvae	3·1	21·0	15	1·1	9·5	11	0·6	18·4	6
Formicoidea and cocoons	0·05	0·1	4	17·7	18·3	7	77·5	36·1	4
Other insects	4·1	2·5	17	4·3	7·5	12	1·4	5·5	8
Araneida	2·5	0·7	12	1·8	1·4	11	2·0	3·1	9
Phalangida	1·2	2·2	4	0·4	0·7	3	0·6	6·1	2
Other animals	—	—	—	0·4	0·7	3	0·6	4·6	9

From this table we may attempt to estimate the importance of the different groups of animals eaten. In the first week, only the larva of the weevil *Phytonomus* is eaten abundantly, frequently, and occupies a large volume in the crops. This species, according to Dr K. G. Blair, is probably *variabilis*, a common pest on clover and trefoils, on the leaves of which it feeds. These larvae are also an important item in the second week food. The larvae of Lepidoptera are also to be regarded as important contributors to the chick diet, for, though few are actually eaten, they occur in more than half of both first and second week crops and occupy a relatively large volume. On the other hand, the springtail, *Sminthurus viridis*, though eaten abundantly and often, occupies but little volume. Nevertheless, since it is evident that the chicks spend much of their time in catching this minute insect, it must also be regarded as an important item in the first and second week crops. Similar remarks apply to the Aphididae (with which are included in this table the Aleyrodidae). The Homoptera (excluding aphids) and the spiders, however, though eaten regularly and occurring in the majority of crops, are never abundant nor do they occupy much volume. Thus though regular items in the diet of partridge chicks they may be of relatively little importance.

As already pointed out, however, most of the important species found are those commonly present in the grass and clover habitats from which our specimens came. This applies particularly to *Phytonomus* and *Sminthurus*. Partridge chicks living in growing corn might show a different selection of insects, dependent on those most commonly available.

In the third week the most abundant insect food is composed of ants and their cocoons. These, however, are not eaten regularly. On hot days in July the ants and cocoons are very close to the surface of the nests, so that partridges have little difficulty in finding them. Once such a nest is opened the young partridge would be able to eat large numbers of ants and cocoons at one meal. The habit of eating ants and their cocoons is retained during adult life (**1**). Apart from this habit the eating of insects in general is probably a random process, the species most abundantly eaten being those most numerous or most easily available in the partridge habitat.

5. SUMMARY

The contents of sixty-nine partridge chick crops were analysed, mostly from grass, clover and lucerne habitats. During the first 2 weeks after hatching the food is predominantly animal, during the third week a change occurs and from 3 weeks onward, food is almost entirely vegetable. Feeding on insects is probably random, the most important forms eaten being larvae of clover weevils, larvae of Lepidoptera, the springtail, *Sminthurus viridis*, Aphididae and ants. In evaluating the various constituents of the crops as to their importance as food, it was found necessary to consider not only the number of each species eaten, but also the volume and frequency of occurrence.

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ON THREE BIRD CENSUSES IN WOODLAND IN NORTHERN RHODESIA

By J. M. WINTERBOTTOM

(*With* 1 *Figure in the Text*)

The censuses which form the subject of this paper were made by the method employed by the Americans whose figures are summarized by Forbes & Gross (**1**, and the papers cited in the bibliography therein) and by me in 1933, in a small count in scrub-woodland (**5**). On a front of 20 yd. every bird seen was counted. The routes followed native paths, but as the country was entirely uninhabited and only one party, of three people, was met, the results are unlikely to have been affected by human interference. The first count was made in the Chindeni hills between 8 and 9 a.m. on 23 October 1937. The day was overcast and rather cold. The distance covered was 4·6 miles (a cyclometer on a bicycle was used to measure distances), which gives an area of 33·5 acres. The second count was made north of Sasare between 7 and 8.45 a.m. on 30 October, over 7 miles (area, 51 acres). The day was clear and hot. The third count was along the south-eastern flank of the Chindenis on 3 November, between 8 and 9 a.m. The distance covered was 3·5 miles, giving an area of 25·5 acres. The day was hot.

These counts were made at the end of the dry season—indeed, the coolness of the air on the first day was undoubtedly due to rain having fallen somewhere within a radius of 50 miles.

The country through which the routes passed is composed almost entirely of *Brachystegia* woodland, mostly fairly well grown, with a sparse undergrowth of grass over which fires had passed. In occasional more open places, the grass was longer and here and there were clumps of bamboo, and anthills, with thickets of *Bauhinia* and other shrubs. The country is hilly and the ground for the most part plentifully sprinkled with large stones and fragments of rock. There was no surface water. These hills on which the third count was done are much lower than the others, with a larger percentage of relatively open country. As will be seen from the accompanying map, the greater part of the area lies in the eastern portion of the Petauke district, in the basins of the Lusangazi and Lusandwa rivers, both of which flow into the Luangwa, the latter by way of the Lupande. The confluence of the Luangwa and the Lupande is, however, off the map. The altitude is between 2500 and 3000 ft.

The total number of species in each census shows that although an hour's counting gave a very similar number of species, this was only about two-thirds of the total number in the region. On a total area of 110 acres, 287 birds were seen in three and three quarter hours. They belonged to at least 51 species (some individuals were not identified). This gives an average of 2·6 birds per acre,

according well with previous African results, as given by R. E. and W. M. Moreau (**2**) and by me (**4**), (**5**). The barren and waterless country apparently

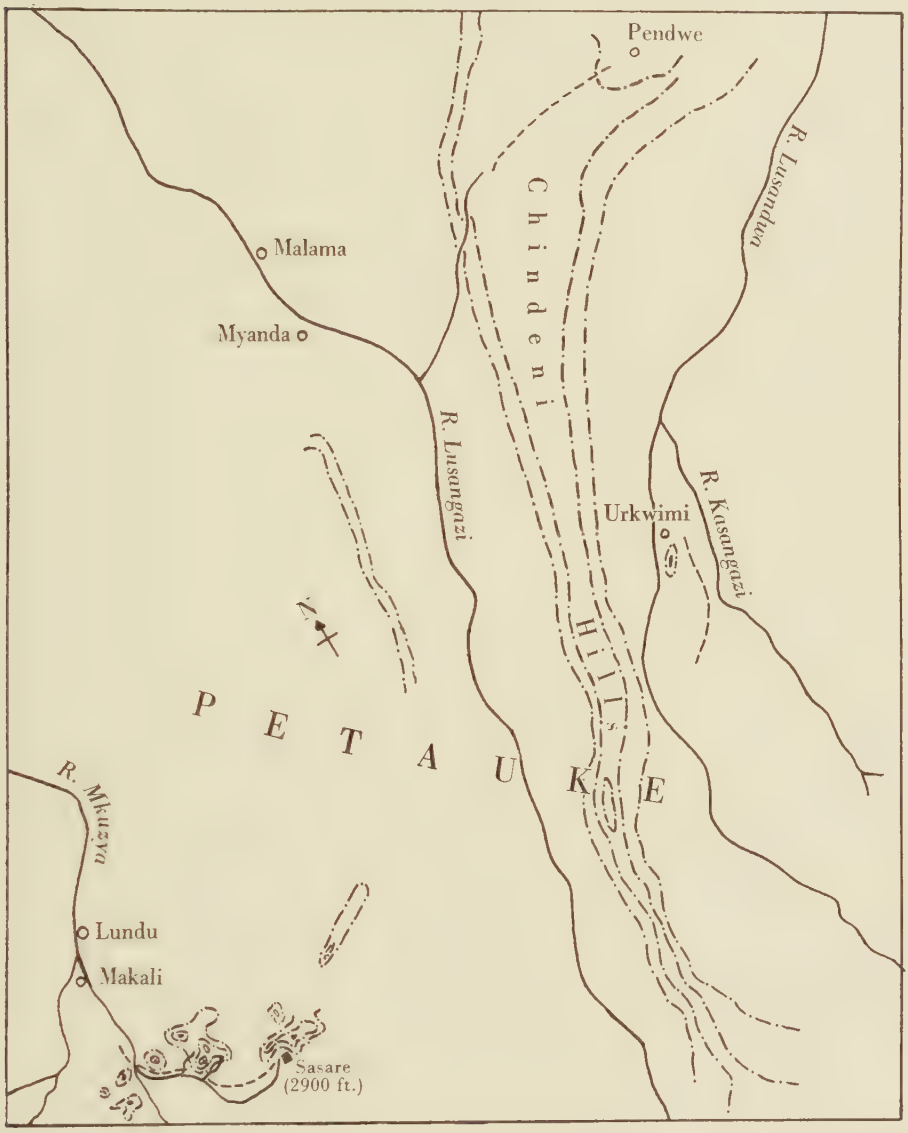

Fig. 1. Rough sketch-map of census region. (Scale ≒ 6·6 miles per inch.) Broken lines show census routes. Form-lines shown by dot and dash are very rough indications.

supports nearly as big a bird population as the mixed Tanganyika area investigated by the Moreaus. Only two species of Palaearctic migrants were included in the counts, the willow warbler (*Phylloscopus trochilus*), which was represented by eight individuals, thus standing ninth in order of abundance;

and the European bee-eater (*Merops apiaster*), of which a single example out of a party came within the area. The most numerous species was the Nyasa cordon-bleu (*Uraeginthus angolensis niassensis*), of which 31 examples were recorded, 24 of them in the third count, where the prevalence of thickets gave it the type of country best suited to it.

Second in order of abundance was the scarlet-chested sunbird (*Chalcomitra senegalensis gutturalis*), with 18 individuals. Next came the ubiquitous yellow-vented bulbul (*Pycnonotus tricolor* subsp.), with 15 examples.

Four other species are represented by ten or more individuals. Of the green-capped Eremomela (*E. scotops pulchra*) and the buff-breasted sunbird (*Cinnyris venustus falkensteini*), 13 examples of each were counted, while 10 each of the drongo (*Dicrurus a. adsimilis*) and the puff-back shrike (*Dryoscopus cubla hamatus*) were seen. All these species are common in woodland, the drongo being a wide-ranging species found almost everywhere. The first and the last two are amongst the commonest members of the bird parties that are such a characteristic feature of the woodland.

A list of all the species seen, with notes, arranged in the order followed by Sclater (**3**), is given on pp. 269-70.

The only really unexpected species in the whole census was the Palm-swift (*Cypsiurus parvus myochrous* (Rchw.)), but this is very common in places in the Luangwa valley where there are borassus palms (*Borassus aethiopium* Mart.) and wanders at times as far as Fort Jameson, where I recorded it six times between July 1932 and March 1935 (**6**).

It is important to realize that the figures obtained by this method of counting are only comparable if we assume that the relative speeds of the moving birds and the moving observer are constant. If the method is used to estimate actual bird density, we would have to assume that the rates of movement were roughly the same in birds and man. If birds were moving five times as fast as the observer, the density of birds would appear five times as great as if they moved at the same speeds. The bird parties, when not alarmed, move definitely more slowly than a walking man, probably not more than 2 miles an hour. The densities estimated are therefore lower for these species than in reality. For other species, such as doves and thrushes, there are as yet no data by which to check this point.

Summary

1. Three bird censuses made at the end of the dry season over strips of hilly woodland country covering 110 acres in the Eastern Province of Northern Rhodesia gave 287 birds of 51 species, an average of 2·6 per acre.

2. This agrees well with previous results for Africa.

3. The most abundant species was the cordon-bleu (*Uraeginthus angolensis niassensis* Rchw.), which was represented by 31 examples; six other species were represented by 10 or more individuals.

Species	Day 1	Day 2	Day 3	Total	Notes
Bateleur (*Terathopius ecaudatus* (Daud.))	.	.	5	5	Mainly an open country species
Lizard-buzzard (*Kaupifalco monogrammicus meridionalis* (Hartl.))	.	.	1	1	
East African shikra (*Accipiter badius polyzonoides* (Smith))	.	.	1	1	The commonest small hawk
Helmet-guineafowl (*Numida m. mitrata* Pall.)	.	.	6	6	A party
Cape turtle-dove (*Streptopelia capicola tropica* Rchw.)	2	.	1	3	Generally, the commonest dove
Blue-spotted wood-dove (*Turtur afer kilimensis* (Mearns))	.	1	.	1	A woodland species, unexpectedly scarce
Goaway-bird (*Corythaixoides c. concolor* (Smith))	.	.	1	1	An open country form
Brown parrot (*Poicephalus meyeri transvaalensis* Neum.)	2	2	.	4	The common parrot
Racquet-tailed roller (*Coracias s. spatulatus* Trim.)	3	.	.	3	
Broad-billed roller (*Eurystomus afer pulcherrimus* Neum.)	.	3	.	3	
European bee-eater (*Merops apiaster* L.)	1	.	.	1	
Grey-headed kingfisher (*Halcyon leucocephala swainsoni* Smith)	.	1	.	1	
Crowned hornbill (*Lophoceros melanoleucos suahelicus* Neum.)	.	1	.	1	A low level form, in the main; note no *L. nasutus*
East African wood-hoopoe (*Phoeniculus purpureus marwitzi* (Rchw.))	.	1	.	1	
Palm-swift (*Cypsiurus parvus myochrous* (Rchw.))	6	.	.	6	A foraging party from low levels
Black-collared barbet (*Lybius torquatus* subsp.)	.	.	1	1	
Yellow-fronted tinker-bird (*Pogoniulus chrysoconus extoni* (Layard))	1	1	2	4	
Greater honey-guide (*Indicator i. indicator* (Sparrm.))	2	.	.	2	
Cardinal woodpecker (*Dendropicus f. fuscescens* (Vieill.))	.	.	1	1	The common woodpecker
Arrow-marked babbler (*Turdoides jardinei kirki* (Sharpe))	4	.	2	6	
Yellow-vented bulbul (*Pycnonotus tricolor* subsp.)	5	6	4	15	
Pallid flycatcher (*Bradornis pallidus murinus* Finsch & Hartl.)	.	2	3	5	
Black flycatcher (*Melaenornis p. pammelaina* (Stanl.))	1	.	.	1	
Chin-spot flycatcher (*Batis m. molitor* Hahn & Küst.)	1	3	3	7	
Red Paradise flycatcher (*Tchitrea perspicillata plumbeiceps* (Rchw.))	.	3	.	3	Migrant; only present Sept. to March
Nyasa Kurrichane thrush (*Turdus libonyanus niassae* Rensch.)	2	2	1	5	
Willow warbler (*Phylloscopus trochilus* (L.))	4	2	2	8	
Green-capped Eremomela (*Eremomela scotops pulchra* (Boc.))	8	5	.	13	

Species	Day 1	Day 2	Day 3	Total	Notes
Tawny-cap grass-warbler (*Cisticola fulvicapilla ruficapilla* (Smith) ; *muelleri* Alex.)	1	.	.	1	
Tawny wren-warbler (*Prinia mistacea graueri* Hart.)	6	.	3	9	
White-breasted cuckoo-shrike (*Coracina pectoralis* (Jard. & Selby))	1	.	.	1	
Glossy-backed drongo (*Dicrurus a. adsimilis* Bech.)	4	1	5	10	
Southern helmet-shrike (*Prionops poliocephala* (Stanley))	7	.	.	7	One party
Puff-back shrike (*Dryoscopus cubla hamatus* Hartl.)	2	6	2	10	
Black-headed bush-shrike (*Tchagra senegala mozambica* (v. Som.))	.	2	1	3	
Sulphur-breasted bush-shrike (*Chlorophoneus sulfureopectus similis* (Smith))	1	.	.	1	
Black tit (*Parus niger* subsp.)	4	.	.	4	Race probably *insignis* Cab.
African golden oriole (*Oriolus auratus notatus* Ptrs.)	.	1	3	4	Chiefly a passage migrant, except in low level riverian cover
Black headed oriole (*Oriolus monacha larvatus* Licht.)	.	5	.	5	The resident woodland oriole
Greater blue-eared glossy starling (*Lamprocolius chalybaeus sycobius* Hartl.)	1	.	4	5	
Scarlet-chested sunbird (*Chalcomitra senegalensis gutturalis* (L.))	9	5	4	18	
White-bellied sunbird (*Cinnyris talatala* Smith)	.	2	.	2	A low level species
Buff breasted sunbird (*C. venustus falkensteini* Fischer & Rchw.)	5	8	.	13	Essentially a woodland species
Rock-sparrow (*Petronia superciliaris* (Blyth))	3	.	1	4	
Yellow-winged Anaplectes (*Anaplectes rubriceps* (Sund.))	5	2	.	7	A woodland species
White-winged whydah (*Coliuspasser a. albonotata* (Cass.))	.	4	3	7	A low level form
Bronze mannikin (*Spermestes cucullatus scutatus* Heugl.)	3	.	.	3	
Nyasa fire-finch (*Lagonosticta rubricata haematocephala* Neum.)	1	3	.	4	
Nyasa cordon-bleu (*Uraeginthus angolensis niassensis* Rchw.)	3	4	24	31	
Mozambique serin (*Serinus m. mozambicus* (Müll.))	7	.	.	7	
Yellow breasted bunting (*Emberiza f. flaviventris* Stephens)	.	3	2	5	Essentially a woodland species
* Not identified (?)	7	7	3	17	
Total individuals	112	86	89	287	
Total species	31	27	26	51	

* This line has been inserted in proof without consultation with the author in view of a discrepancy found in the totals—Eds.

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THE FAUNISTIC RECOVERY OF A LEAD-POLLUTED RIVER IN NORTH CARDIGANSHIRE, WALES

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(*With* 1 *Figure in the Text*)

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1. Introduction

This study concerns the Rheidol, which is the largest river in north Cardiganshire, and along the course of which are some 43 mine workings (Map). The lead-mining industry here goes back to pre-Roman times; in the latter part of the nineteenth century it suffered severely from competition with larger undertakings, and shortly before the Great War all the mines had ceased working. During 1914–18 a few mines were reopened, but after the War these soon closed down once more. This paper is a study of the progressive recovery of the river fauna which followed.

The River Rheidol has its source on the western side of Plynlimon, the stream (Nant-y-llyn) from Llyn Llygad Rheidol being joined in the neighbourhood of Nant-y-moch by a number of mountain streams (Afon Hengwm, Afon Hyddgen, Afon Llechwedd Mawr and Afon Camdwr), and flows thence in a general southerly direction to Ponterwyd and Devil's Bridge, where it turns sharply westwards to reach the sea at Aberystwyth. The local rocks are grits, flags and shales of the Valentian and Bala series; metalliferous veins occur along the fault lines usually running east-north-east to west-south-west and are usually in the upper parts of the basins of the principal rivers.

Like all the rivers of the district, the Rheidol is rapid in flow, cutting deep gorges in the middle part of its course, and for the most part its bed is stony. Its lower valley is covered with boulder clay, and in quiet reaches its waters

are slightly turbid with the resulting mud; but for the most part the waters are clear and rapid and the banks are strewn with gritty pebbles brought down in time of flood. The general character of the river is such as to suggest that trout, salmon, etc., might occur in abundance. The neighbouring rivers, Dyfi, Leri and Teify, which are remarkably similar to the Rheidol in general physical character, have such fisheries and it is recorded in oral evidence taken in 1872 by the Commissioners on Rivers Pollution (1874*b*, p. 76) that early in the nineteenth century the Rheidol was a healthy river abounding in fish. However, when the study of the river was begun by Dr Carpenter in 1919, the lower reaches (below Rhiwfron) were absolutely devoid of fish life, the invertebrate fauna was extremely poor both in variety of species and number of individuals, and the vegetation was limited to slight coatings of moss and liverwort on some of the stones, and a certain amount of the Algae *Batrachospermum* and *Saccheria*.

The barren condition of the river has always been attributed to the extensive lead-mining, crushing and washing operations which have been carried on upon the banks of the river and some of its tributaries for hundreds of years past, though it is stated that serious pollution did not enter until the introduction of fine grinding machinery early last century. After this innovation, and despite the introduction of systems of settling ponds, a considerable amount of fine, lead-containing slimes found its way into the river. During periods of flood, when the water spread over the surrounding land, this material formed a film of mineral material over the vegetation, and numerous cases of poisoning of horses, cattle and poultry were attributed to this cause.

In the *Report* of the Rivers Pollution Commission appointed in 1868 are given a number of analyses of samples of water which had passed through settling ponds. The following example is taken therefrom (1874*a*, p. 42; and Frankland 1877, p. 834):

> Submitted to subsidence, 11·72% of the slime contained in the turbid water leaving the last settling pond at the "Powell United" lead mine near Aberystwyth, was deposited in the first 15 minutes, and 56·7% in the next six hours, leaving 31·58% still in suspension. 100 parts of the slime suspended in this water contained 1·38 part of lead as galena; but after subsidence for six hours and a quarter only 0·45 part of lead as galena remained in suspension. In connexion with this sample it is necessary to remark that the subsidence to which it had been submitted in the settling-ponds was more than usually effective, as is seen from the fact that 100,000 parts of the turbid water contained only 82·52 parts of suspended matter, whilst in the muddy waters from other mines more than 400 parts have been observed.

Whatever may be the physiological effect of these galena-containing slimes on domestic animals eating polluted vegetation, it has been proved by Carpenter (1924*a*, 1925) that the old theory, which attributed the killing of fish in polluted rivers to laceration of the gills and inflammation caused thereby by particles of galena grit, is without foundation. Her work has established beyond doubt that the poisoning of fish is due to the presence of the salts of certain heavy metals *in solution*. As a result of experiments in the field and in

the laboratory, it is concluded that these metals (in ionic state) react with some constituent of the mucus secreted by the gills with the formation of an impermeable pad over the latter, so that respiration is impeded and the fish dies of suffocation. As an example, it may be quoted that a concentration of 4 parts per 10 million of lead in water causes fatal results in minnows (*Phoxinus phoxinus*) in 36 hours. In still lower concentrations the time is longer and the fish may be able to get rid of the impeding film on the gills as rapidly as it is formed.

The solubility of lead sulphide (galena) is very low, and a saturated solution contains only 2·5 parts of lead per 10 million (the corresponding number for zinc sulphide—blende or black jack—is 4·0 parts per 10 million). It is obvious, therefore, that solutions of galena and blende can, as such, have no poisonous action on fish. It has been shown that galena when exposed to the combined action of air and water—which will obviously be much accelerated by vigorous agitation such as occurs in mine separation plants—is slowly oxidized to lead sulphate which has a solubility in water corresponding to 31·5 parts of lead per million. This explains why the effluents from active mine plants contain on the average 3 parts of lead per million in solution.

If slimes from an active mine are allowed to pass into a river the process of oxidation and solution of the resulting sulphate goes on continuously. The same process will occur on dumps of mine refuse which are such a prominent feature of the middle reaches of the Rheidol. During fair weather the oxidation will proceed and the oxidation products remain *in situ* until the first floods dissolve the sulphates and carry them into the river.

Fortunately, in course of time, the fine-grained material on the surface of many of the dumps becomes caked into a hard impenetrable mass from which water flows off before causing much action. Where the dump material is coarser and allows water to penetrate through, afterwards reappearing at the base of the dump as streamlets during prolonged wet weather, the amount of dissolved salts may be considerable. With the cessation of mining operations a river, therefore, tends to recover itself. By the action of floods the fine uncaked material may be washed from the dumps into the river and thence to the sea, while the heavier mineral particles tend to settle in the deeper and quieter parts where oxidation is prevented or delayed.

For the last nineteen years the Lower Rheidol has been kept under observation. The main changes which have taken place in the transition from an almost dead river to one supporting a relatively normal animal population are summarized below.

2. Surveys from 1919 to 1926

From 1919 to 1926 the work was done by Dr Kathleen Carpenter, who recorded her results in various papers (notably 1924*a*, 1925, and 1927*a*). During the period 1919–21 a thorough examination resulted in the finding of

only 14 species, distributed as indicated in Table 1. The list is almost entirely composed of insects and a few crustacean species. Vertebrata, Mollusca, Hirudinea, Oligochaeta and Platyhelmia are absent. During this period a number of estimations were made of the dissolved lead content of the river, the results varying from 2 to 5 parts per 10 million of water.

Table 1. *Species recorded from the Lower Rheidol previous to May* 1922 (*Carpenter*, 1924*a*, *p.* 14)

Crustacea (Copepoda, Ostracoda)	3	Plecoptera	2
Arachnida	1	Ephemeroptera	1
Hemiptera	2	Neuroptera	1
Coleoptera	2	Odonata	1
		Diptera	1
		Total no. of species	14

In the late spring of 1922 there was a long period of drought, and the level of the water fell considerably and many of the smaller tributaries dried up. The last two of the few mines that had been reopened during the War ceased working in 1920 and 1921 respectively. After the period of drought a number of further estimations were made of the diffusible lead content. From 24 October 1922 to 16 March 1923 it was nil in the majority of samples, and even in time of flood did not rise above 1 part in 10 million. (It should be noted, however, that later critical methods of estimating lead, at present in use, were not developed at this time.)

Following the improvement in the physical condition of the river came an almost immediate improvement in the fauna and flora. The previous Algal and Bryophyte vegetation was considerably augmented and at Penybont and elsewhere masses of *Callitriche verna* and *Ranunculus aquatilis* appeared. More striking still was the improvement in the fauna; the number of species was doubled and species previously recorded appeared in vastly greater numbers. Eight species of Trichopteran larvae appeared, and the flatworm *Polycelis nigra* was also taken, being the first planarian to be recorded from the Rheidol. The new conditions were traced 5½ miles upstream to Capel Bangor.

The species, increased to 29 in number, were distributed as in Table 2.

Table 2. *Species collected in the Lower Rheidol in and after May* 1922 *and up to March* 1923 (*Carpenter*, 1924*a*, *p.* 14)

Platyhelmia	1	Plecoptera	2
Crustacea (Copepoda, Ostracoda)	4	Ephemeroptera	2
Arachnida	1	Neuroptera	1
Hemiptera	2	Odonata	1
Coleoptera	4	Diptera	3
		Trichoptera	8
		Total no. of species	29

In the spring of 1924 two yearling trout were placed in a cage in the Rheidol, just above Capel Bangor, and survived from 4 February to 24 March, during which period the presence of lead was not determinable in the river.

Between 22 and 24 March heavy rain fell; on the 24th the lead content was 4 parts per 10 million and the fish died with the characteristic white film of mucus over the gills. (This increased amount of lead is explainable owing to the temporarily resumed workings at Erw-tomau.) This is the last record of so high a degree of pollution. From 1 June to 8 October in the same year six fish survived in the cage at the same place, no lead having been determinable in the water during this period. From this time onwards the Lower Rheidol is regarded by Carpenter as being chemically pure, though it must be borne in mind, as already indicated, that the critical methods of determining lead, which are at present in use, were not developed at this time.

Carpenter gives no later records of the fauna of the Rheidol as such, but (1927*a*) lists under the single heading "longer rivers of coastal area" the species from both the Lower Rheidol and Lower Ystwyth, the latter being a river with a very similar pollution history to that of the Rheidol. The combined list contains 57 species.

During the following year or two it appeared to us that further recovery might have taken place, and accordingly we carried out a further faunistic survey in some detail, from July 1931 to May 1932. Observations on the lead content were made concurrently by Prof. Campbell James. The survey resulted in the collection of 103 species, a remarkable increase; while the estimations of Prof. James indicated the intermittent continuance of a very low lead content.

3. Faunistic survey of the lower rheidol, 1931–2

(*a*) *The regions examined*

A. *Penybont.*

The majority of the samples were taken just above Penybont bridge near Llanbadarn fawr, about a mile and a half from the mouth of the river at Aberystwyth. Above the bridge the river, which here is moderately shallow, runs a fairly rapid straight course for about a quarter of a mile. On the left side the water is of almost uniform depth, the bed is stony and there is little vegetation; but on the right side the bank, though not notched into large backwaters, is very irregular, and accordingly the river is broken up into numerous small regions, in some of which the depth is about 3 ft. close to the bank and the water comparatively slow moving, the bed being sand with large clumps of *Callitriche verna* and *Ranunculus aquatilis* growing in it. Around the fringe of these pools there is generally a fair amount of submerged grass (*Glyceria fluitans*). In the grass and waterweed of these areas numbers of mayfly nymphs, water beetles, and caddis larvae shelter. Many species, such as the naiad of the dragonfly *Cordulegaster annulatus*, live almost in the sandy bed. Here and there the water moves so slowly that there are deposits of dead leaves and other debris on the bottom, where numerous species shelter.

This stretch is easily the most richly populated area of the river, at any rate as far up as Capel Bangor. All the species listed were found in the Penybont

area except *Planaria vitta*, *Haemopis sanguisuga*, *Elmis aeneus* (all three species from Capel Bangor only), *Hydroporus erythrocephalus*, *Dytiscus punctulatus* (both from Parc-y-llyn only), and *Phryganea* sp. (Whitebridge only).

B. *The Whitebridge.*

At the white concrete bridge over the Rheidol, about half a mile above Llanbadarn, a portion of the river is separated from the main stream by a small island so that a kind of backwater is formed. This has a wide opening to the river near the bridge, and a narrow inlet higher up, through which the water enters to keep up a steady but slow flow through the backwater. This flow is always present even when the level of the river is below normal, and in flood

Fig. 1. Map of the River Rheidol and its tributaries. × Lead mines; ← sampling stations (*A*, *B*, *C*, *D*).

time the flow is almost as rapid as that of the main stream. The bottom of the backwater is chiefly covered with stones, dead leaves and other debris; near the bank are large beds of submerged grass, and here and there are clumps of *Callitriche verna* and *Ranunculus aquatilis*. However, it is the submerged grass (*Glyceria fluitans*) that shelters most of the fauna of this area. The species are essentially the same as those found at Penybont, but the number of individuals of some of the more quiet-water living species is greater. The single specimen of *Phryganea* sp. was taken here.

C. *Near Capel Bangor.*

Near Capel Bangor, about 5½ miles from its mouth, the Rheidol makes an extremely acute bend. Near the apex of the angle and under the right bank, there is a deep pool where the water is almost stationary. Masses of *Callitriche*

verna grow upon the sandy bottom, which is carpeted with dead leaves from the overhanging trees, and other debris. Here the water net readily captures a great variety of species. A little higher up the river is shallow and rushes rapidly over large stones. Here web-spinning Trichoptera occur in great numbers, and almost every stone is plastered with *Simulium* larvae. This is the only part of the river where we have found *Planaria vitta*, *Elmis aeneus*, and *Haemopis sanguisuga* (a single specimen only of the last). *Rhyacophila* sp. occurred here in abundance, in contrast with its small numbers in the other three regions.

D. *Backwaters near Parc-y-llyn farm* (*Aberystwyth flats*).

About a quarter of a mile nearer the sea than Penybont bridge, and near Parc-y-llyn farm, the right bank of the river is indented by three small backwaters. These are generally in communication with the main stream, but there is very little circulation of water in them, and when the water-level is low they are separated off and become stagnant pools. In flood time, however, the river rushes through them, and so it is probable that any chemical changes that take place in the river at flood time exert their effect on the fauna of these regions just as much as upon that of the main stream.

Samples taken from these backwaters show that they are populated almost entirely by the same species that live in the main stream, the essential difference being that certain species, found rarely in the main stream, occur in the backwaters in large numbers—due apparently to the greater abundance of vegetation and the greater placidity of the water. Thus, *Limnaea pereger*, rarely found in the flowing waters of the main stream, occurs in numbers in the backwaters. Its presence here can hardly be due to any chemical distinction between the waters of the two regions, as it is also found in numbers in the Whitebridge Backwater, where it lives in water apparently identical chemically with that of the main stream.

These backwaters support masses of Algal and Bryophyte vegetation, in addition to *Callitriche verna*, and their bottoms are covered with mud and dead leaves in which live numbers of *Chironomus* larvae and Oligochaeta. Frogs spawn here, and in the spring countless tadpoles grow up and invade the main stream. Newts also occur, and insects usually associated with stagnant pools, such as *Hydrometra stagnorum* and *Nepa cinerea*. The beetles, *Hydroporus erythrocephalus* and *Dytiscus punctulatus*, were found only in this region.

(*b*) *Methods of investigation*

No precise quantitative sampling was attempted. Attention has been concentrated on collecting as many species as possible, whether common or rare, and noticing their general abundance, distribution and seasonal variation. The great majority of the species were taken in the water net, a few were taken

under stones, and a very small number by sieving out sand and mud from the bottom.

Each sample was taken in the following manner: First, specimens were captured of all surface dwellers such as *Gerris* and *Gyrinus*, and their general abundance noted. Then numbers of stones were taken up at various places, the animals on them captured; samples of the sand and mud on the bottom were brought home for sieving; and a canvas water net was thoroughly worked through the submerged grass and clumps of waterweed. The whole contents of the net were brought to the laboratory for thorough examination, all the species recorded, and notes were made of their relative abundance. All samples were taken in the same manner so that the results are reasonably comparative.

(*c*) *Number of samples*

July 1931. Four from A, one from C, two from D.

October 1931. One per week from A, one per week from B, one from C.

November 1931. One per week from A, one from B, three from D.

December 1931. As November until 22 December. No samples were taken between 22 December and 8 January.

January 1932. Two per week from A, one per week from B, one from C.

February 1932. As January.

March 1932. One per week from A, one from B.

April 1932. As March.

May 1932. One per week from A, two from B, one from D. Last sample taken 28 May.

(*d*) *Species recorded*

The species recorded in the 1931–2 survey are listed in Table 3, which also gives their relative and seasonal abundance. Our thanks are accorded to Prof. E. Balfour-Browne for help in naming the Coleoptera. The identification of the nymphs of Plecoptera, and Ephemeroptera, and Trichopteran larvae presents difficulties in the present state of knowledge; we thank Mr Martin E. Mosely for advice in dealing with the Trichopteran larvae, and Mr D. E. Kimmins, similarly, in regard to the nymphs of Ephemeroptera and Plecoptera, and for his identification of the species of Ephemeroptera which we have bred out. We have put after each named species the reference to a description with which our specimens are in agreement. These references are listed at the end of this paper. Specimens of nearly all the species have been preserved, and are being deposited in the British Museum (Natural History).

During the few years prior to the survey trout (*Salmo trutta*) had occasionally been seen in the river. In May 1932 they were observed as high up as Aberffrewd, about 7 miles from the river mouth, and lower down they were sufficiently abundant to lead to some fishing just above Penybont Bridge and at Aberystwyth flats. It was reported that a couple of sewin were taken in the latter region in August 1932.

Table 3. *Relative and seasonal abundance of species collected in the Lower Rheidol, July* 1931 *to May* 1932

A. Abundant. Large numbers in each sample.
B. Fairly numerous. Say 5–10 specimens in each sample.
C. Less common. Say 2–5 specimens in each sample.
D. Rare. Say 1 specimen in each sample.
E. Very rare. Only 1 specimen during the whole month.

Species	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
PLATYHELMIA									
Polycelis nigra Ehrenb. (**2**)	C	C	C	C	C	C	C	C	C
Planaria vitta Dugès (**1**)	.	.	.	.	D	D	.	.	.
OLIGOCHAETA sp.	C	C	C	C	C	C	C	C	C
HIRUDINEA									
Glossosiphonia complanata L. (**3**, p. 74)	.	.	.	D	D	.	D	.	.
Herpobdella atomaria Carena (**3**, p. 81)	.	.	.	.	D	D	.	E	.
Haemopis sanguisuga L. (**3**, p. 79)	.	.	.	.	E	.	.	.	.
MOLLUSCA									
Pisidium sp. (**5**, p. 7; **5a**, pl. 3)	.	.	.	.	C	C	C	C	D
Limnaea pereger Müller (**4**, p. 104)	.	.	.	.	.	C	.	C	B
Ancylastrum fluviatile Müller (**4**, p. 113)	.	.	.	.	.	E	.	C	.
Zonitoides nitidus Müller (**4**, p. 240)	.	.	.	.	.	E	.	.	.
CRUSTACEA									
Cyclops sp.	C	C	C	C	C	C	C	C	C
EPHEMEROPTERA									
Baetis sp. (**6**, p. 32)	.	.	A	A	A	A	B	.	.
Siphlonurus lacustris Etn. (bred out)	A	.	.	.	.	B	A	A	A
Ecdyonurus sp. (**6**, p. 31)	.	.	.	C	B	B	A	A	A
Leptophlebia sp. (**6**, p. 31)	.	.	.	.	.	.	.	C	D
ODONATA									
Cordulegaster annulatus Latr. (**7**, p. 31)	.	.	.	.	D	C	.	.	.
Pyrrhosoma nymphula Sulz. (**7**, p. 121)	.	.	.	C	B	C	C	C	D
Agrion puella L. (**7**, p. 116)	.	.	.	C	B	C	C	C	D
PLECOPTERA									
Perlodes sp. *a* (**8**, p. 83; **10**, p. 286)	.	.	C	B	B	C	.	.	.
Chloroperla sp. *a* (**8**, **10**)	.	.	E	E	C	B	C	C	D
Nephelopteryx nebulosa L. (**8**, p. 90; **10**, p. 305)	.	.	E	.	.	.	.	.	.
Isopteryx sp. *a* (**8**, p. 88; **10**, p. 300)	.	.	.	.	.	.	C	C	C
Leuctra sp. *a* (**8**, p. 92)	.	.	D	C	C	B	B	C	D
Protonemura sp. *a* (**8**, p. 93)	C	C	B	B	B	B	D	.	.
Amphinemura cinerea Morton (syn. *A. cinerea* Oliv. **8**, p. 95)	.	.	.	C	C	C	.	.	.
Nemurella inconspicua Pict. (syn. *N. pictetii* Klp. **8**, p. 95)	.	.	.	.	.	.	E	.	.
HEMIPTERA									
Hydrometra stagnorum L. (**9**, p. 148)	C	.	.	.	.	.	.	C	C
Gerris lacustris L. (**9**, p. 156)	C	.	.	.	.	.	.	C	C
G. najas De G. (**9**, p. 154)	D	.	.	.	.	.	.	.	C
Velia currens Fab. (**9**, p. 149)	A	B	.	.	.	.	.	.	C
Nepa cinerea L. (**9**, p. 327)	.	.	.	D	D	.	.	.	D
Notonecta glauca L. (**9**, p. 329)	B	B	B	.	.	.	B	B	C
Corixa geoffroyi Leach (**9**, p. 333)	B	B	.	.	.	.	.	.	C
Corixa sp. *a*	C	.	.	.	.	.	.	.	.
Corixa sp. *b*	.	.	B	B	B	B	C	.	.
Corixa sp. *c*	.	.	B	B	B	B	B	B	B
Corixa sp. *d*	.	.	.	.	C	.	.	.	.
Corixa sp. *e*	.	.	.	.	.	.	.	D	.
NEUROPTERA									
Sialis sp. (**10**, p. 321)	.	.	.	C	C	B	B	C	.
LEPIDOPTERA									
Sp. larva	.	.	.	.	.	E	.	.	.

Table 3 (*cont.*)

Species	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Trichoptera									
Rhyacophila dorsalis Curt. (bred out)	D	D	D	D	C	C	D	D	.
Hydropsyche sp. *a*	.	.	D	C	C	C	C	D	D
Polycentropus flavomaculatus Pict. (**11**, p. 230)	C	C	C	B	B	B	C	D	.
Plectrocnemia conspersa Curt. (**11**, p. 230)	.	.	.	C	C	.	.	.	.
Beraeodes minuta L. (**11**, p. 243)	.	.	.	C	C	C	D	D	.
Phryganea sp. *a* (**11**, p. 238)	.	.	.	.	.	E	.	.	.
Sericostoma personatum Spence (bred out)	.	.	.	D	C	C	C	D	D
Limnophilus marmoratus Curt. (bred out)	.	.	.	C	B	B	C	C	D
Limnophilus sp. *a*	E	.	.	.	.	.	.	E	.
Limnophilus sp. *b*	.	.	.	E	.	.	.	.	.
Limnophilus sp. *c*	.	.	.	.	.	D	D	.	.
Limnophilus sp. *d*	.	.	.	.	.	.	.	D	.
Limnophilus sp. *e*	.	.	.	.	.	.	.	D	.
Anabolia nervosa Leach (**11**, p. 256) (bred out)	A	.	.	.	.	C	B	B	A
Halesus sp. *a*	.	.	.	C	B	A	A	B	.
Gen. *a*, sp. *a*	D	.	.	C	C	C	.	E	.
Glossosoma sp. *a* (pupa) (**11**, p. 290)	.	.	.	D	.	.	.	.	.
Coleoptera*									
Haliplus ruficollis De G. (**12**, p. 155; **14**, p. 16)	C	C	.	.	.	.	.	.	.
H. lineatocollis Marsh. (**12**, p. 156; **14**, p. 17)	C	C	.	.	.	.	D	.	.
H. wehnckei Gerh. (**14**, p. 18)	.	.	.	.	.	.	.	C	.
Haliplus sp. *a*	C	.	.	.	.	.	.	.	.
Laccophilus interruptus Panz. (**12**, p. 161)	.	.	.	.	.	.	E	.	.
Deronectes latus Steph. (**12**, p. 170)	.	.	.	.	.	D	.	D	D
D. elegans Panz. (**16**; **16a**, p. 177)	.	.	.	D	C	C	D	D	C
D. 12-pustulatus F. (**12**, p. 171)	C	.	.	D	.	.	C	C	C
Coelambus inaequalis F. (**12**, p. 168)	.	.	.	.	.	.	E	.	D
Hydroporus pictus F. (**12**, p. 176)	C	C	C	C	C	.	D	C	C
H. palustris L. (**12**, p. 182)	B	B	B	B	B	B	B	B	B
H. lepidus Ol. (**12**, p. 177)	.	.	.	C	C	B	B	C	C
H. vittula Er. (**12**, p. 181)	.	.	.	.	.	.	E	.	.
H. rivalis Gyll. (**12**, p. 177)	.	.	.	.	.	.	.	D	.
H. davisii Curt. (**12**, p. 178)	.	.	.	.	.	.	.	D	.
H. erythrocephalus L. (**12**, p. 182)	.	.	.	.	.	.	.	C	C
Hydroporus pubescens Gyll. (**12**, p. 185)	.	.	.	.	.	.	.	.	E
Hydroporus sp. *a*	D	.	.	.	.	.	.	.	.
Ilybius fuliginosus F. (**12**, p. 198)	C	C	.	.	.	.	.	C	C
I. ater De G. (**12**, p. 199)	.	.	.	.	.	.	.	.	E
Agabus bipustulatus L. (**12**, p. 196; **14**, p. 19)	.	.	.	D	.	D	D	.	.
A. didymus Ol. (**12**, p. 193)	.	.	.	D	C	C	C	D	C
A. sturmii Gyll. (**12**, p. 195)	C	C	.	.	D	C	D	.	D
Platambus maculatus L. (**12**, p. 197)	C	.	.	E	.	E	.	.	D
P. maculatus L. larva ? (**15**, p. 37)	.	.	.	.	.	.	.	.	.
Colymbetes fuscus L. (**12**, p. 203)	.	.	.	.	.	.	.	D	E
Dytiscus marginalis L. (**12**, p. 205)	D	.	.	.	.	.	.	D	D
D. marginalis larva (**12**, p. 204)	C	.	.	.	C	C	C	C	.
D. punctulatus F. (**12**, p. 204)	.	.	.	.	.	.	.	.	E
Helophorus viridicollis Steph. (**14**, p. 31)	.	.	.	E	.	.	.	.	.
Helophorus sp. *a* (**12**, p. 233; **14**, p. 29)	D	.	.	.	.	.	.	.	.
Laccobius alutaceus Thoms. (**14**, p. 27)	.	.	.	E	.	.	.	.	.
Gyrinus natator Scop. (**12**, p. 215)	B	C	.	.	.	.	.	C	B
Gyrinus sp. larva (**12**, p. 211)	.	.	.	D	D	C	.	.	.
Elmis aeneus Mull. (**13**, p. 376)	.	.	.	.	.	.	D	.	.
E. volkmari Panz. (**13**, p. 376)	.	.	.	C	C	C	D	D	.

* Examples of all the forms to which specific names are here assigned have been seen and confirmed by Prof. F. Balfour-Browne, with the exception of *Dytiscus marginalis* (larva and imago), *Dytiscus punctulatus*, *Gyrinus natator*, and the specimens of *Elmis*. The material was not all submitted to him, so that the writers alone are responsible for the indication of seasonal occurrence. The (coleopteran) specimens are imagines, except where otherwise stated.

Table 3 (*cont.*)

Species	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
DIPTERA									
Tipula sp. (**19**, p. 944; **18**, p. 68)	.	.	.	.	D	D	.	.	.
Tabanus sp. (**19**, p. 946; **18**, p. 149)	.	.	.	.	D	D	.	D	.
Simulium sp. (**19**, p. 946; **17**, p. 176; **18**, p. 107)	A	B	C	C	C	B	B	.	A
Chironomus sp. (**19**, p. 945; **17**, p. 139)	B	B	B	B	B	B	B	B	B
Tanypus sp. (**19**, p. 945; **17**, p. 152)	C	C	C	C	C	C	C	C	C
Ceratopogon sp. (**19**, p. 945; **17**, p. 155)	.	.	.	D	D	.	.	D	.
ARACHNIDA									
Hydracarina	.	.	.	.	.	.	.	C	B
VERTEBRATA									
Anguilla anguilla L. (as *Anguilla vulgaris* in **21**, p. 241; **22**, p. 49)	B	.	.	.	.	D	C	C	C
Gasterosteus aculeatus L. (**20**, p. 238; **22**, p. 61)	C	C	C	C	C	B	B	B	B
Triturus vulgaris vulgaris L. (syn. *Molge vulgaris*, **23**, p. 68; **24**, p. 38)	D	.	.	.	.	D	D	D	D
Rana temporaria temporaria L. (tadpoles) (**23**, p. 89)	B	.	.	.	.	.	.	B	B
R. temporaria temporaria L. (frogs) (**23**, p. 73; **24**, p. 39)	.	.	.	.	.	.	C	C	.

(*e*) *Relation of lead concentration to the fauna*

During the period of the survey Prof. Campbell James periodically examined samples of water from the Lower Rheidol, using critical methods. A large number of analyses were made of river water taken under various conditions at different points in the region surveyed. Under normal conditions dissolved lead to the amount of 2 parts per 100 million was present, rising to 1 part per 10 million during flood periods. The lead concentration was never found to exceed the latter figure. The following are representative analyses:

Date	Station	Condition of river	*p*H	Total solids (Parts per 100,000)	Lead (Parts per 10,000,000)
14 Aug. 1931	Penybont Bridge	Full flood	6·6	4·6	1·0
20 Aug. 1931	Aberystwyth Flats	Flood cont.	6·6	4·5	1·0
23 Oct. 1931	Lovesgrove	Medium	6·7	5·0	0·5
6 Jan. 1932	Aberystwyth Flats	Full flood	—	9·0	1·0
10 Feb. 1932	Aberystwyth Flats	Low water	—	—	0·2
21 June 1932	Aberystwyth Flats	Low water	6·7	3·6	0·2
28 Oct. 1932	Aberystwyth Flats	Medium after flood	6·7	3·4	0·3

The water at Aberystwyth flats during a flood period, 31 March 1932, contained 2·6 parts per 100,000 of filterable solid material in suspension. Analysis of this suspended matter indicated that it contained 2 parts per 10 million of lead, 19 parts per million of iron, the remainder being silica (estimated on the volume of filtered water). The filtered water contained 0·25 part of lead per 10 million. This result indicates that the suspended matter contains only very slight traces of lead.

The remarkable increase in the richness of the fauna would thus appear to be associated with the persistence of conditions with only a reduced amount of lead in solution. It was evident, however, from the analyses of Prof. James that the river was still liable to slight intermittent pollution as a result of heavy rains washing out lead sulphate from the lead dumps; but the lead content of the river never rose to the relatively high values reached up to 1924.

This was due mainly to the closing down of the mines. And although the mine dumps still remained a source of pollution, it appeared likely that time had lessened the danger of pollution from this source. While great reserves of galena doubtless still remain deep down in the dumps it is possible that the lead near the surface has been largely removed, and that consolidation of the surface and the growth of vegetation has tended to hinder access of the weathering agents to the reserves.

When a flood occurs it is generally of short duration, the river level returning to normal in 3 or 4 days, or at most, a week. One of the writers (J. R. E. Jones) has shown that under laboratory conditions a lead concentration of 1 part in 10 million is directly fatal to the stickleback, *Gasterosteus aculeatus*; but an exposure of 14 days is necessary, on an average, before death occurs. If the fish is removed from the solution a reasonable time before death, and placed in untreated water, complete recovery occurs. Thus it appeared that the existence of this fish in the river depended on the shortness of the pollution periods. It is quite possible that a period of very heavy rain extending over 2 or 3 weeks might maintain the lead content of the river at 1 part per 10 million for this long and destroy all the sticklebacks in the river. No such period of prolonged flood occurred during the period under review.

The summer of 1936 was unusually wet, and was followed by an autumn of heavy rainfall. During October, November and December of the same year the river, though not actually in flood, was for long periods much above its normal level. The chances of pollution from the mine dumps were thus at a maximum and it was thought desirable, therefore, to carry out a further survey following this period. This survey was done by Mr Harry Evans, a Zoology Honours student, under the supervision of the writers, during the period December 1936 to April 1937 inclusive. Samples were taken at approximately fortnightly intervals from two (A and B) of the four stations surveyed in 1931–2. Only 68 species were recorded as against 104 species in the 1931–2 survey; but these comprise all the commoner forms found in the earlier period, including the stickleback, and the difference in number is due to the absence of many of those forms which occurred but rarely in the earlier survey. This might be expected, since Mr Evans's samples were 11 in number and collected from two localities compared with 74 samples in 1931–2 from four localities.

The number of individuals present, as distinct from the number of species, was of the same order as at the time of the earlier survey and the absentee species cannot be considered as of significance in relation to pollution. We can say with confidence that the river retains the healthy condition evidenced in 1932, in spite of heavy rain and periods of high water-level. Chemical evidence is entirely in agreement: in July 1937 Prof. James reported that while one, at least, of the streamlets which flow from the mine dumps into the river continued to be polluted with lead, the dilution by the mainstream was so great that there was no detectable degree of pollution of the river in any part of its course.

One of the writers has shown (Appendix) that the stickleback is among the animal forms most sensitive to lead, so that the river is not only free now from danger from lead pollution to its fauna during normal periods, but even the heaviest floods which are likely to occur seem to be without appreciable effect.

Nevertheless, as compared with some rivers, the fauna is not rich, and for this an explanation other than that of metallic pollution must be sought. The stream is swift and there is a lack of silt in its bed; there is a remarkable scarcity of lime; and the *p*H is low. Crustacea, Mollusca, and Hirudinea are very poorly represented. In laboratory experiments, however, the leech, *Haemopis lateralis*, survived for 18 days in a 3 parts per million solution of lead. The scarcity of Crustacea and Mollusca may well be associated with the scarcity of lime. The *p*H of the water has been observed at Penybont and elsewhere from time to time, and varies between 6·6 and 6·8.

At the time of writing (October 1937) young sticklebacks are observable in considerable numbers at Penybont, as also are large numbers of *Ancylastrum fluviatile*, another of the forms most sensitive to lead. We may conclude that the fauna of the Lower Rheidol has very materially, perhaps fully, recovered from the effects of the metallic pollution from which it suffered in association with the lead-mining industry.

4. Summary

1. From 1919 to 1921, the Lower Rheidol River only yielded 14 species of animals, all of them Arthropoda, in a careful survey made by Carpenter. During this period estimations of dissolved lead in the water revealed the presence of 2–5 parts of lead per 10 million of water.

2. From 1922 to the present time it would appear that lead has been indeterminable, or in the order of 2 parts per 100 million, except during flood periods. In one such period in 1924 Carpenter recorded 4 parts per 10 million, but no estimation exceeded 1 part per 10 million during the 2 years following. From June 1931 to the present time no greater flood concentration than 1 part in 10 million has been observed by Prof. James.

3. With the reduction in the amount of dissolved lead has been associated a steady improvement in the fauna. During the year following May 1922 the number of species recorded by Carpenter increased to 29, while the survey of July 1931 to May 1932 yielded 103 species, a fauna which appears to have remained stable since.

4. The Appendix gives the survival times of a number of species in a 3/1,000,000 solution of lead (as lead nitrate). The figures have some value as suggesting indices of pollution.

5. The stickleback (*Gasterosteus aculeatus*), which is one of the most sensitive to lead of the animals found in the Rheidol, was found, in laboratory experiments, to be killed after 14 days exposure to 1 part lead per 10 million of water.

This is the maximum concentration which has been observed in the Lower Rheidol for some years, even during flood, and the normal content is of the order of only 2 parts per 100 million, a concentration that the fish seems able to withstand indefinitely. It would appear therefore, that, provided no abnormal flood periods occur, there should be little direct danger to fish (at any rate, stickleback) life. And from the 1936–7 survey, made after a summer of exceptionally heavy rainfall, it appears that even when the river continues well above its normal level over long periods, there is now no appreciable effect upon the fauna. This has recovered very materially, we think fully, from the effects of the metallic pollution. Since 1932, trout have been sufficiently abundant to lead to some fishing.

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APPENDIX

THE RELATIVE SENSITIVITY OF AQUATIC SPECIES TO LEAD IN SOLUTION

By J. R. Erichsen Jones

The field work of Carpenter (1924*a*, 1925) has established that there is a certain amount of correlation between the lead content of streams and the fauna they support. In slightly polluted waters (3 parts per 10 million) fish are eliminated, but the invertebrate fauna seems to be little affected. As the pollution becomes more serious the Mollusc *Ancylastrum fluviatile* is eliminated, then other Mollusca, Platyhelmia, and Crustacea Malacostraca. With further increase in the lead content Oligochaeta, Trichoptera and Hirudinea disappear, so that the fauna comes to consist of certain adult and larval insects and entomostracan Crustacea only. Finally, in the most highly polluted waters near the mines, containing 3 to 6 parts per million of lead, larvae of the midge *Tanypus nebulosus* and nymphs of the mayfly *Chloëon simile* appear to be the sole survivors.

Attempts have been made to estimate the relative sensitivity of a variety of aquatic species by laboratory experiments. Several series of experiments have shown that the maximum concentration of lead that the stickleback can withstand indefinitely is less than 1 part lead per 10 million of water. Tadpoles (*Rana temporaria temporaria*) are considerably less sensitive, and appear to be unaffected by lead at concentrations below 1 part per million.

The following is a typical experiment: 500 c.c. volumes of solution were employed, in wide mouthed jars and four tadpoles placed in each; four were placed in a similar volume of untreated tap water as controls. The tadpoles were about 20 mm. in length (tail included), they were not fed, and the solutions were not changed. The survival times were as follows:

Concentration (Parts lead per parts water)	Average survival time days
5/1,000,000	1·75
3/1,000,000	5
1/1,000,000	6·75
5/10,000,000	11·75
Controls	9

Thus a concentration of 1 part per million appears to have a lethal effect. No lethal effect was ever observed at concentrations lower. Increase of solution volume produced no change in the general result. Tadpoles of smaller size appeared to be slightly more sensitive, those larger, slightly more resistant.

It was not found possible to determine, in this way, the critical concentration for a large variety of aquatic species; but it is not unreasonable to suppose that the relative sensitivity of a variety of species will be to some extent

Table 4. *Approximate average survival times in lead nitrate solution (Three parts lead per million of water)*

*p*H of solution 6·4

Species		Average survival time	Average survival time of controls days
Limnaea pereger Müll.	A	4 hr.	About 30
Gasterosteus aculeatus L.	A	12 ,,	,, 25
Ancylastrum fluviatile Müll.	B	15 ,,	,, 5
Simocephalus sp.	A	2 days	,, 3
Cyclops sp.	A	3 ,,	,, 3
Simulium sp.	B	4 ,,	,, 7
**Rana temporaria temporaria* L. (tadpoles)	B	5 ,,	,, 9
Sphaerium corneum L.	A	5·3 ,,	Over 70
Chironomus sp.	B	5·4 ,,	,,
Triturus vulgaris vulgaris L. (young with external gills)	A	6 ,,	,,
Chloëon simile Eat.	B	6 ,,	,,
Tubifex tubifex Müll. (small colony with mud)	—	7–10 ,,	,,
Corixa geoffroyi Leach	A	14 ,,	,,
Velia currens Fab.	A	17 ,,	,,
Agrion sp.	B	17 ,,	,,
**Haemopis sanguisuga* L.	A	18 ,,	,,
Anguilla anguilla L.	A	21 ,,	,,
Larval Dytiscidae	B	27 ,,	,,
Planaria vitta Dugès	B	40 ,,	,,
Agabus bipustulatus L.	A	40 ,,	,,
Dytiscus marginalis L.	A	49 ,,	,,
Hydroporus palustris L.	A	50 ,,	,,
Notonecta glauca L.	A	70 ,,	,,
Polycelis nigra Ehrenb.	B	70 ,,	,,

The experiment was discontinued after 70 days, all the animals in the solutions having died. In the case of each species in which the average survival time of controls is given as over 70 days the majority of these were alive at the end of the experiment.

In all cases, except those marked with an asterisk, the survival times are means of six experiments, i.e. six individuals of each species were placed in the solution and six in tap water, as controls. In the cases marked with an asterisk the survival times are means of four experiments.

A, 1000 c.c. of solution not changed throughout experiment. B, 50 c.c. of solution in uncovered Petri-dish renewed daily.

indicated by their relative survival times in a lead solution of a concentration similar to that of the polluted streamlets. Accordingly, using lead solution of concentration 3/1,000,000 (that found in heavily polluted waters near the mines), a series of survival time determinations was made. These are given in order of increasing survival time in Table 4. Survival times of controls are also given, and it will be seen that the result is somewhat complicated by the fact that a number of the species only exist for a limited time in the control water, though in some of such cases (e.g. *Ancylastrum*) the difference in survival time between the animals in the lead solution and the controls is quite significant. Where this complication does not arise, and the controls live indefinitely, the series compares moderately well with the field observations of Carpenter, with

certain notable exceptions, of which the most conspicuous are the Planarians, *Planaria vitta*, and *Polycelis nigra*. No Trichoptera were included in the experiments: Carpenter's field observations indicate that their degree of resistance is of the same order as that of oligochaetes and leeches. It will be observed that the eel is considerably more resistant than the stickleback, and that, of the Invertebrata, the Mollusca are decidedly the most sensitive, while the insects, especially the species breathing atmospheric oxygen, are the most resistant. *Notonecta glauca* survived 25 days in a lead solution of concentration as high as 50 parts per million, and in one experiment a number of large larvae of *Dytiscus marginalis* were kept for 5 weeks in a 20/1,000,000 solution, feeding voraciously on tadpoles during the whole period. After this time they pupated, but none metamorphosed successfully.

NOTES ON THE BIOLOGY OF THE FAEROE MOUSE (*MUS MUSCULUS FAEROENSIS*)

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(*With Plate* 11 *and* 1 *Figure in the Text*)

1. Introduction

Under the auspices of the Oxford University Exploration Club an expedition visited the Faeroe Islands during the summer of 1937. One of the objectives was a study of the Faeroe mouse, and the resulting material is offered in this paper. Collecting apparatus included 48 live traps of the Tring type (**4**) and a number of "break-back" traps; these, however, were not very successful, as they were continually being disturbed by puffins (*Fratercula arctica*). The majority of the mice were caught in simple native traps—small wooden boxes with a trigger and falling door. A total of 48 specimens was secured (14 living and 34 dead) of which 19 were males and 29 females. All the dead specimens were measured; the skins and skulls of 23 have been deposited with the Bureau of Animal Population in Oxford. The living mice were brought back to the Zoological Society of London and to the Bureau of Animal Population.

We should like very much to thank the following for assistance: Mr Charles Elton and the Bureau of Animal Population; the British Museum and the Zoological Society of London; Prof. R. Spärck and Dr Magnus Degerbol of the Zoologiske Museum in Copenhagen and Dr F. Fraser Darling for personal communications; and the people of the Faeroes who helped us to secure the specimens.

2. Historical

The first known record of mice in the Faeroe Islands is that of Debes (**6**), which dates back to 1673. Landt (**13**), who lived in the islands from 1792 to 1798, reported the mice as being displaced by the rat. As the islands have been inhabited for over 1000 years, it is difficult to say how long the mice may have been there, but by Landt's time they were sufficiently well known to form part of the legend and folklore of the natives. The Faeroe mouse was first described and named in 1904 by Eagle Clarke (**5**) from five specimens obtained on Nolsö by Annandale & Marshall (**1**) in the preceding year. The type is to be found in the Royal Scottish Museum in Edinburgh. It was originally described as a subspecies, *Mus musculus faeroensis* Clarke, and was so considered by Millais (**14**) and Trouessart (**17**); but Miller (**15**) has given it the status of a full

species. Following this lead, Barrett-Hamilton & Hinton (**3**) refer to it as such, "pending further research".

3. Distribution

The Faeroe Islands (Fig. 1) can be divided into three groups: north-eastern, central and southern. A letter from Prof. Spärck of Copenhagen indicates that

Fig. 1.

mice are found in each group, i.e. on the following islands: Fuglö in the north-east; Myggenaes, Strömö, Österö and Nolsö in the central group; and Sandö and Syderö in the south.[1] With the exception of Syderö, which we did not visit, our observations substantiate this. Prof. Spärck's letter also gives the distribution of the brown rat (*Rattus norvegicus*), which differs strikingly as follows: Viderö, Kunö and Bordö in the north-east; Vaagö, Strömö and Österö in the central group; Hestö and Syderö in the south. We could find no traces of the black rat (*Rattus rattus*), a common species in Landt's time.

The Faeroes are important geographically as the outermost connecting link between Europe and Iceland. Such importance is perhaps minimized in the case of the mice, which are carried by human agencies. Most of the boats put

[1] During recent years mice have appeared in the houses on Hestö (information received Aug. 1938).

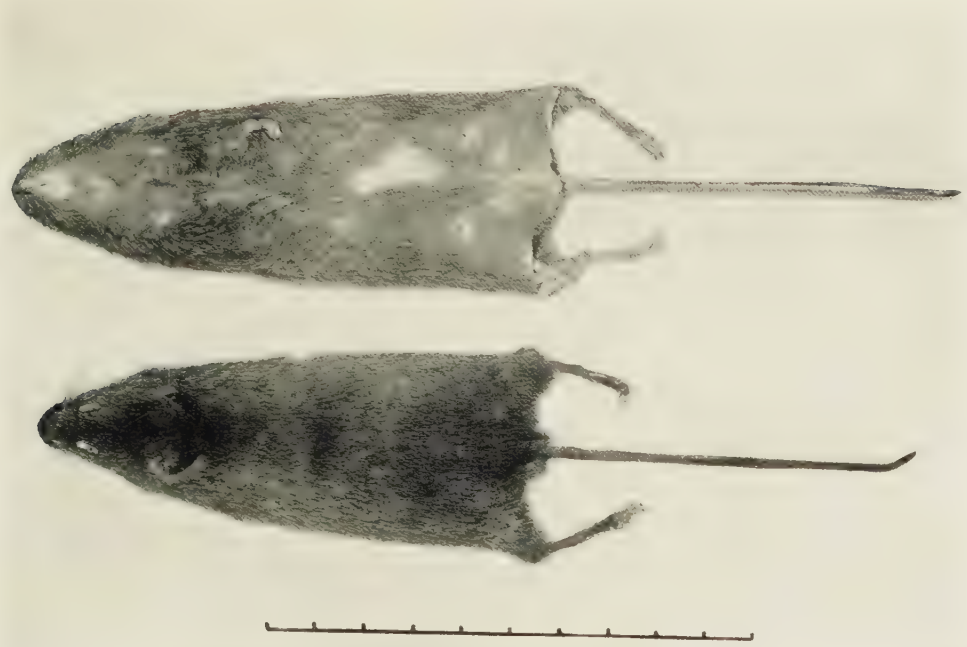
into the Faeroes on their way to and from Iceland. Miller has recorded a series of *Mus musculus* from Reykjavik. The islands do not boast of many good harbours, and the calls made by vessels are few though fairly regular. There is considerable communication among the separate islands, but this is largely by small boats which in many cases cannot dock at all. Myggenaes and Fuglö, with their great cliffs on all sides, are typical of the majority of the islands. The opportunity for isolation to have effect is a good one, in view of the fact that the Faeroe mouse has been there for at least 250 years. A comparable case covering a much shorter period of time is recorded by Jameson (**11**).

4. Forms and status

(*a*) *Forms.* The question arises as to whether there is more than one form of mouse in the Faeroes, i.e. are the mice from the cliffs and the fields the same as those in the villages? The islanders believe there are two forms. One of us examined the Faeroe mice in the Copenhagen Museum and was impressed with the relatively small size and dark colour of the specimens from Thorshavn, the largest town and the main harbour of the islands. These differences are also noted by Annandale (**1**). It is possible that the population of Thorshavn mice may be replenished with fresh stock arriving on boats. However, there is no evidence of any such difference in our material from the islands.

(*b*) *Mice on Fuglö.* On Fuglö, the easternmost of the islands and the only one of the north-eastern group where mice are found, we collected 27 specimens. Of these 19 were peculiar in possessing an irregular but strikingly conspicuous white patch on the middle of the belly (Pl. 11, phot. 1); otherwise they appeared typical of the Faeroe mouse. This aberration was present in both sexes and was characteristic of both immature and adult pelage. For this reason it would appear to be inherited, and experiments are now in process to determine the genetics of the problem. The Fuglö population of mice is almost completely isolated, a fact which helps to explain the existence of this peculiarity in 70% of the samples collected. What significance for survival value, if any, can be attached to this variation is impossible to say. The suggestion of Ford (**9**), that non-adaptive visible effects of a mutation may be associated with physiological changes or with some other invisible "factor", may well be applicable here. At any rate, here would seem to be further evidence of the effects of isolation.

(*c*) *Status.* Under the present circumstances it is impracticable to determine the proper status of the Faeroe mouse. Miller's treatment of *M. musculus* and its allies is far from satisfactory and has been criticized in a recent paper by Zimmermann (**19**). Miller's conclusions regarding *faeroensis* were drawn from six specimens, which he found to differ "so conspicuously from all other known members of the group that, however recent the animal's origin may have been, there seems no doubt that the form is a distinct species". The only distinguishing characters given are a larger size, and more robust form and skull; there are no peculiarities of form or structure. The colour, originally



Phot. 1. *Mus musculus faeroensis* from Fuglö. Above, female, No. 24, ventral view. Below, female, No. 3, dorsal view. Scale in cm.
N.B. Note clarity of detail obtained by preparation of skins as flat mounts (see Elton **8a**).

Phot. 2. *Mus musculus faeroensis* from Nolsö (type locality). Above, male, No. 30, dorsal view. Below, female, No. 33, ventral view. Scale in cm.

described as rufous and grey-black on the upper surface, buff and pale grey on the belly, is regarded by Miller as closer to that of *M. musculus* than to that of another related island form, the St Kilda mouse, *M. muralis* Barrett-Hamilton (**2**). The tendency towards robustness is reflected in the development of the stout hind feet. Dr Winge of Copenhagen suggests (see Eagle Clarke (**5**)) that this feature is connected with the mouse's activities among the rocks of the bird cliffs, where some of the original specimens were caught. However, both the Faeroe wren and starling show a similar tendency. In determining the proper status of the Faeroe mouse, it will be necessary to consider the significance of geographical isolation and its effect.

5. Ecological discussion

(*a*) *Habitat.* A great effort was made to secure mice from the bird cliffs, but only one of our collection can accurately be said to have come from there. This was found in a sheep hut on the bird cliffs. Several were taken in the cultivated maerkland and in outbuildings bordering the fields, but the majority were caught in houses in the various villages. As the latter were collected by the natives in their own traps, there is no means of obtaining a statistical analysis of the habitats. The difficulties of collecting on the cliffs were admittedly great, and small colonies might well have escaped notice. An extensive search was made for dung and other signs, but on only one occasion was any discovered. Further investigation of this problem is greatly to be desired. However, it is certain that the villages are important centres of the mouse population, a fact not sufficiently stressed by previous workers, who emphasized the cliff habitats.

(*b*) *Habits.* The one locality in which dung was discovered was in the entrance to a puffin burrow on Myggenaes. Thomas (**16**) reports a wild form of *M. musculus* from Portugal living in association with *Apodemus sylvaticus*, and suggests that the house mouse occupies the burrows of the wood mouse. (*Apodemus* is not found on the Faeroes, however.) The puffins form large colonies of subterranean nests on the slopes above the steep cliffs. The mice that live there apparently do so in association with these birds, whose constant coming and going in countless thousands upset many of the traps and made collecting almost impossible. Both the birds and the burrows would provide excellent protection. Whether the mice remain there after the puffins have gone and throughout the winter is impossible to say. The people both affirmed and denied this belief. The climate is temperate enough to allow for survival during the colder periods of the year.

The experience of Fraser Darling with house-mice on the Treshnish Isles, Argyll, seems very relevant here, and with his permission we include the following report:

Lunga of the Treshnish Isles has been uninhabited by human beings for about 80 years. We went there on 25 August 1937, and pitched our tents near the dry stone walls of the old

houses on the north-east corner of the island. Three days later the first house mouse came into the tent and was drowned in a bowl of water. It was indistinguishable, as far as I could see, from the common house mouse of the mainland.

After that, we were much troubled by the mice and we caught 75 by the time we left at the end of November. We moved camp 50 yd. into a brackeny hollow early in October and the mice were at us again in two days. We saw one old and scabby mouse on the shingle at the shore level at the extreme north point of Lunga. This was ¼ mile away from the old houses and 90 ft. lower.

We were impressed by the immediate return of these mice to house habits. They were far cheekier and more inquisitive than *Apodemus* would have been in similar circumstances and they did their best to take up permanent quarters in the tent.

Elton (**7**) also found that Hebridean house mice normally occur out-of-doors, at least during the summer. They are likewise found living wild in America and Australia. Such facts indicate considerable adaptability as a species, doubtless contributing to a wide distribution. At the same time Fraser Darling's report suggests a habitat preference for domestic conditions, which would tend to keep the house mouse in association with man and act as a retarding influence upon the colonization of new territory away from buildings.

(*c*) *Food.* The Faeroe mouse seems to be almost omnivorous. The villages offer a variety of food in the form of refuse, as well as household stores of meat and grain. The situation on the bird cliffs is quite different, however. A stomach analysis of the specimen taken from the sheep-hut on the cliffs revealed bits of feathers. Within the puffin burrows, possible sources of food include eggs, feathers and refuse of the birds, as well as a small insect population, chiefly Coleoptera, our collection of which has been described by Commander Walker (**18**). The dominant grass, *Festuca ovina*, presumably produces a good quantity of seed which is a potential food supply.

(*d*) *Breeding.* Examinations were made of all the dead females. Three of these contained seven embryos each; a fourth specimen contained only two. One of the living females produced two young, but ate them several days later. Of the total number of females nine weighed over 30 g. each, with two records of over 40 g. each. They were all caught between 17 July and 22 August.

The breeding experiments at the Bureau of Animal Population with mice from Fuglö have not yet been successful, as only the island stock is being used. At the Zoological Society of London a female Faeroe mouse was crossed with a male English house mouse, and a litter of four young was born on 5 April 1938.

(*e*) *Parasites.* All the mice were examined for external and internal parasites. A naked eye examination of the internal organs proved negative. Three ectoparasites were recorded, as follows:

On mice from Nolsö, 22–23 August 1937

Acarina: E 1. *Pergamasus crassipes* Linn.

E 2. *Haemogamasus michaeli* Oudemans.

Siphonaptera: E 3. *Nosopsyllus* (*Ceratophyllus*) *fasciatus* Bosc.

The latter is the common rat flea and is recorded from the St Kilda mouse by Harrisson & Moy-Thomas (**10**) and from *Mus musculus* in the Isle of Lewis, Outer Hebrides, by Elton (**7**). It was not included in the list of *Siphonaptera* recently published in the Zoology of the Faeroes (**12**). Prof. Spärck informs us

Table I. *Measurements of Faeroe mice*

Locality	Date (1937)	Collector's no.	Wt. (g.) (including any embryos)	Length (mm.) Head and body	Tail	Hind foot	Ear
A. Females							
Myggenaes	26 July	2*a*	41·5	—	—	—	—
Nolsö	21 Aug.	M	Over 40	—	—	—	—
Fuglö (Kirke)	11 ,,	7*	39	98	86	18	15
Nolsö	22 ,,	26*	37·5	93	91	19	15
Fuglö (Kirke)	12 ,,	24*	36	88	84	18	14·5
Sandö (Sand)	5 ,,	E	36	—	—	—	—
Myggenaes	17 July	B†	34	—	—	—	—
Nolsö	22 Aug.	28‡	30·5	97	88	18·5	15
Myggenaes	27 July	2	30	102	86	18	15
Fuglö (Kirke)	12 Aug.	I	28·5	—	—	—	—
Nolsö	24 ,,	33	27	96	88	18·5	14·5
Fuglö (Kirke)	11 ,,	9	26	90	84	20	15
,,	12 ,,	J	24·5	—	—	—	—
,,	11 ,,	8	23	94	85	19	14
,,	12 ,,	22	22·5	92	86	18·5	15·5
,,	12 ,,	H	22·5	—	—	—	—
Sandö (Sand)	5 ,,	F	22	—	—	—	—
Fuglö (Kirke)	11 ,,	5	21	86	79	18	14
,,	12 ,,	19	21	85	83	17·5	14
,,	12 ,,	23	21	—	—	—	—
,,	11 ,,	3	19	89	77	17·5	14
Nolsö	23 ,,	32	19	84	74	17·5	13
Myggenaes	26 ,,	C	18·5	—	—	—	—
Nolsö	21 ,,	29	11·5	—	—	—	—
Fuglö (Kirke)	11 ,,	12	10·5	63	65	16·5	12·5
,,	12 ,,	17	9·5	69	63	18	13
..	11 ..	14	9·5	66	68	18·5	12·5
..	12 ..	20	9·0	—	—	—	—
,,	11 ,,	16	6·0	59	52	16	10·5
B. Males							
Myggenaes	19 July	1	32	98	92	19·5	14
Fuglö (Kirke)	11 Aug.	4	26·5	97	?	17	14
,,	11 ,,	6	25	85	84	18	14·5
Sandö (Sand)	5 ,,	D	24	—	—	—	—
,,	5 ,,	G	24	—	—	—	—
Fuglö (Kirke)	12 ,,	L	23	—	—	—	—
Nolsö	22 ,,	31	21·5	83	76	18·5	13·5
,,	22 ,,	27	21	87	87	18·5	14
Myggenaes	15 July	A	20	—	—	—	—
Nolsö	23 Aug.	30	19·5	81	74	18	13
,,	21 ,,	25	16	83	79	18·5	14
Fuglö (Kirke)	12 ,,	21	16	—	—	—	—
,,	12 ,,	K	14·5	—	—	—	—
Nolsö	21 ,,	N	11·5	—	—	—	—
Fuglö (Kirke)	11 ,,	13	10	69	58	18	13
,,	11 ,,	11	9·5	70	64	19	12
,,	11 ,,	15	8·5	72	64	18	12·5
,,	11 ,,	10	8·5	69	66	19	12·5
,,	12 ,,	18	7·0	63·5	64	18	12·5

* Seven embryos. † Gave birth to two young a few days later. ‡ Two embryos.

that only *Pergamasus crassipes* has been found in the islands before, and that none of the three species has been taken on the Faeroe mouse. Elton (**8**) reports *Haemogamasus michaeli* from *Mus musculus* in the Outer Hebrides, as well as *Pergamasus hamatus* Koch, but not *P. crassipes*. We should like to thank Dr Karl Jordan of Tring and Mr R. J. Whittick of the British Museum for these identifications.

6. Summary

1. An expedition to the Faeroe Islands during the summer of 1937 collected 48 specimens of the Faeroe mouse.

2. Mice have existed there for at least 250 years and are to-day widely distributed, though not found on all the islands. The type locality is Nolsö. The distribution of the brown rat differs strikingly, as shown on the map (Fig. 1).

3. There was no indication of two forms, but a variation with a white patch of hairs on the belly was found in Fuglö.

4. The status of the Faeroe mouse is problematical, an important factor being the significance attached to isolation.

5. The Faeroe mouse has been successfully crossed with the English house mouse.

6. The villages appear to be important centres of populations, with the bird cliffs as marginal habitats where there may be an association with the puffins, which merits further investigation.

7. On the bird cliffs possible sources of food include eggs, feathers and refuse of the birds, a small insect population and a quantity of grass seed.

8. An examination for parasites produced two kinds of mites (Acarina) and one species of flea (Siphonaptera), none of which has previously been taken on the Faeroe mouse. Two are new records for the islands.

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A CENSUS OF BREEDING GANNETS (*SULA BASSANA*) ON MYGGENAES HOLM, FAEROES[1]

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(*With Plate* 12 *and* 1 *Figure in the Text*)

1. Introduction

The earliest reference to the gannet (*Sula bassana* L.) in the Faeroes occurs in the medieval Faeroese ballad "Fuglakvaeði" (**5**), where it is mentioned with a number of other birds, most of which are still common in the islands. This source does not record any breeding place, and at the present time gannets only nest on the holm which lies to the west of the island of Myggenaes, and on the neighbouring stacks, Píkarsdrangur and Flatidrangur. The early works of Debes (**3**), Svabo (**12**), and Landt (**8**) record the position of the colony, but unfortunately do not give any indication of the number of breeding pairs. Landt (1800), probably following Svabo, gives the number of adults killed in April as 200; and the same number of young birds was caught in September. Müller (**9**), writing 62 years later, says that the number of adults and young taken annually was 300 and 600 respectively. Feilden (**4**) visited Myggenaes in 1872, but was unable to cross to the Holm, and Barrington (**2**) in 1892 "estimated the Myggenaes Gannets at 1500", i.e. 750 pairs. Hagerup (**7**) gives photographs but no estimate. Wynne-Edwards, Lockley & Salmon (1936) (**16**) base their figure of 750 breeding pairs on an estimate by Miss Acland (**1**) in 1928, and on the observations of Lockley, who passed close to the colony in June 1935, and estimated that not more than 1000 birds were present.

Salomonsen (**10**) gives no estimate of the total breeding population, but records the number of birds caught annually in recent years as about 450 adults and 850 young. During a visit to Myggenaes in July 1937, the present writers were told by some of the bird-catchers themselves that they only take 600–800 young from the Holm and the two stacks together, of which 150 are caught on Flatidrangur. No adult birds are taken at the present time.

The lack of agreement in these various observations made it desirable to re-examine the status of the Myggenaes colony.

2. The census

The recent censuses of breeding gannets on Ailsa Craig (**14**) and (**15**) have been carried out almost entirely by direct counts from the tops of the cliffs and from the shore (the alighting method has also been used where convenient). The

[1] Gannet Population Studies, No. 4.

nature of the cliff ledges on Myggenaes Holm does not favour the crowded grouping observed on Ailsa Craig, and it was found that on the Holm itself the majority of the nests were placed along a rather broad ledge running along the northern face of the rock, about 100 ft. above sea-level. The remaining nests were mainly in small groups, either above or below this ledge. On Flatidrangur and Píkarsdrangur the birds nest almost exclusively on the summits, which are respectively 81 and 104 ft. above sea-level.

It was found impracticable, and indeed unnecessary, to use the alighting method on Myggenaes Holm, and the results shown in Table 1 are from direct counts by two independent observers. The nests on the main ledges on the Holm and many of the subsidiary groupings were counted from various positions along the tops of the north and west cliffs. The colonies on Flatidrangur and Píkarsdrangur were counted from the pasture land at the south-west corner of the Holm. In a subsequent boat journey round both the Holm and the island, it was possible to include the numbers of the remaining groups on the northern cliffs, and also to reach the summit of Flatidrangur, where the nests were counted at close quarters.

During the last few years there has been a slight spread of the colony on the island of Myggenaes itself. In 1936 and 1937 a single pair of gannets nested on the most westerly point of the island and in both cases a young bird was reared. It should be emphasized, however, that this nest is in full sight of and quite near to the main colony on the Holm, and should in no way be considered as a daughter colony.

The sketch-map (Fig. 1) shows the division of the colony into artificial groups for convenience in counting.

Table 1

	Number of nests	
On Myggenaes	F.C.E.	H.G.V.
On west end	1	1
On Myggenaes Holm		
A	119	120
B	209	209
C	257	250
D	28	28
E	192, 182 } 187	186, 184 } 185
F	211	217
G	224	218
H	35	35
On Píkarsdrangur	122, 118 } 120	116, 110 } 113
On Flatidrangur (count at very close quarters)	232	232
Totals	1623	1608

These figures therefore give the mean number of nests as 1615·5, from which it is concluded that the breeding population of gannets in 1937 was about 3230.

No attempt was made to count the non-breeding birds, which were particularly numerous on some of the main ledges and on part of Flatidrangur.

3. Discussion

From the point of view of population fluctuations the chief interest in the Myggenaes colony lies in the fact that it is one of the few remaining gannetries where birds are captured annually. The number taken rose from 400 in the year 1800, to 900 in 1862, and is now about 600–800. Gurney (**6**) has suggested that the rise in numbers taken in Müller's time (1862) may have been due to "better appliances and greater skill". There seems, however, to be little ground for this suggestion, since the Faeroese fowling

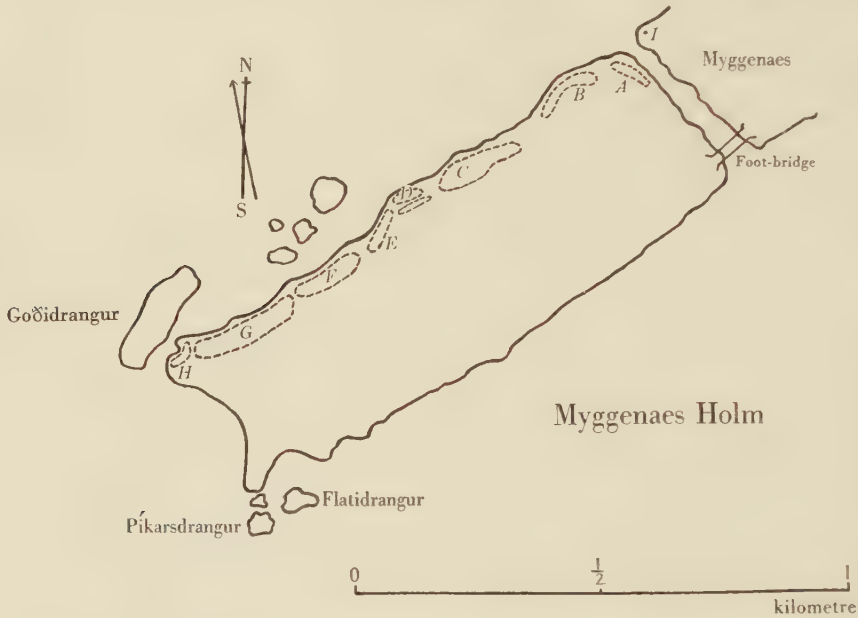

Fig. 1. Sketch-map of Myggenaes Holm (based on the Danish Geodetic Survey).

methods have remained unchanged for centuries. Landt's description (**8**) of the capture of young and adult birds towards the end of the eighteenth century applies almost without modification at the present time.

It may be argued that with the increase in the human population of Myggenaes from 75 in 1801, to 179 in 1925 (**13**), there would be a strong tendency towards an increase in the number of birds taken annually. There are, however, two points against such an argument: (1) as the nesting sites of the gannets are very inaccessible, it would be much simpler to increase the food supply, if it were necessary, by the comparatively easy method of puffin-catching on the bird slopes of Myggenaes itself. It is, indeed, most unlikely that the gannet has ever played a major role in the sea-bird diet of the people of

Photo F. C. Evans

Phot. 1. Flatidrangur and Píkarsdrangur, the two stacks at the west end of Myggenaes.

Photo H. G. Vevers

Phot. 2. Gannets on the summit of Flatidrangur, with the peak of Píkarsdrangur in the right background.

Myggenaes, and nowadays the catch is mainly carried out for "sporting" motives. (2) It is characteristic of the Faeroese fowling methods that great care is taken to guard against any measure of exploitation, which might lead to extermination. It may safely be said that the annual catch would not increase unless a general rise in numbers had been noticed by the fowlers. This may be contrasted with the indiscriminate capture of nestling gannets on Sula Sgeir by men from the Butt of Lewis, in Scotland (**11**).

These facts would suggest that the great increase in the annual capture is an index of increase of the colony as a whole, coincident with the spread of the gannet's breeding range (for example, the new colonies in Shetland), and with a probable increase in the world population of gannets during the last 50 years.

4. Acknowledgements

Our thanks are due to Herr Olaf Heinesen, Herr Pauli Hansen and Herr Abraham Abrahamsen for their assistance on Myggenaes, to Herr Mikkjal Dánjalsson á Ryggi of Bö, in Vaagö, for advice on a number of points, and to Prof. E. S. Goodrich for reading and criticizing the manuscript.

5. Summary

1. Previous records of the Myggenaes gannet colony are reviewed, and an increase in the annual capture during the last 200 years is noted.

2. Details of a census of the whole colony by direct counting are given. From this count it is concluded that the breeding population of gannets in 1937 was 3230.

3. The increase in the annual number of birds taken is probably not correlated with any possible improvements in fowling technique or with the increase in the human population of Myggenaes, but with an increase in the colony as a whole. This increase coincides with a similar fluctuation in the world population of gannets during the last 50 years.

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THE 1938 CENSUS OF GANNETS (*SULA BASSANA*) ON AILSA CRAIG

By H. G. VEVERS and JAMES FISHER

In 1936 (**1**) and 1937 (**2**) censuses of gannets (*Sula bassana* L.) were made on Ailsa Craig, in the former year by means of direct counts, and in 1937 by direct counts and the alighting method. The present census was made by direct counts alone.

The natural and artificial groupings used in the former years have been retained, for the most part without the necessity for any change. We have, however, to add a new group of some 25 nests, situated directly above the "Main Craigs East" (see diagram in **2**). The census was made between 5 and 12 April. The complete results are shown in the following table:

Table 1

Cliff	1938 direct counts: Counts (pairs)	1938 direct counts: Mean	Increase or decrease (compared with 1937)
Barestack	95, 97	96	−
Northwards of Ashydoo	287, 293	290	−
Ashydoo A1	189, 188, 197, 184	189·5	+
,, A2	32, 32, 33, 34	32·75	−
Balvaar	522, 539	530·5	−
Balvaar-Cairn	58, 60, 60	59·33	−
Cairn	606	606	−
Barrheads, S.	38	38	−
,, Mid	19	19	+
,, N.	95	95	+
Cairn-Mare and part of N. Barrheads	452	452	+
Mare	1684, 1692	1688	−
Mare-Stranny Point:			
S1	82, 80, 82	81·33	−
S2	65, 53, 56, 64, 64	60·4	−
S3	108, 115, 123	115·33	−
S4	191, 180	185·5	−
Main Craigs:			
Top	276, 268	272	+
Main Part	403, 404, 400, 398	401·25	+
East	107, 109, 99, 104, 99, 109	104·5	+
Far East	47, 47, 45, 47, 43	45·8	+
East Top (new)	23, 26	24·5	+
	Total = 5387 pairs (approx.)		

The total number of breeding pairs in 1937 was 5945. There has therefore been a decrease of 9·4% (approximately) over the colony as a whole. Among the individual groups of nests the only significant decrease has taken place in the Mare and Cairn. In contrast to this there has been an increase of all the groups on the Main Craigs.

Observations have been continued on the diurnal activity of the gannets, but we are awaiting further evidence before publication.

We are extremely grateful to L. S. V. Venables, Malcolm Stewart and L. P. Madge for their assistance in making counts, and especially for their constructive criticism of census methods. This has resulted in a slight revision of our ideas as to the efficacy and reliability of the alighting method, and we hope to make further and fuller analyses of it.

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GANNETS (*SULA BASSANA*) ON NOSS, SHETLAND, WITH AN ANALYSIS OF THE RATE OF INCREASE OF THIS SPECIES[1]

By JAMES FISHER and L. S. V. VENABLES

(*With Plate* 13 *and* 2 *Figures in the Text*)

1. Previous counts and estimate

Gannets (*Sula bassana* L.) showed interest in the Noup of Noss in 1911 or 1912, Mr G. T. Kay tells us (**18**), and the colony was established in 1914, when one pair is reported by MacPherson (**21**) as having bred. In the following year four pairs bred (**29**). In 1918 three young were reared, and in 1919 there were five pairs (**12**) and in 1920 10 (**35**). In 1930 or 1931 Mr George Russell (**25**) estimated about 200 pairs.

In the world estimate of the numbers of breeding gannets undertaken by Wynne-Edwards, Lockley & Salmon (**8**), the numbers of gannets on Noss in 1934 and 1935 were recorded as in the neighbourhood of 800 pairs. The roughness of this estimate (made by L. S. V. V.) was perhaps not sufficiently stressed by the writers. It was based on the combination of a count of the number of incubating pairs on a control area of cliff, and an estimate of the total density by comparison.

2. Description of the colony

In their paper Wynne-Edwards, Lockley & Salmon gave the impression that "Noss" and the "Noup" were two distinct breeding-cliffs. In fact the Noup is the great cliff, rising to 600 ft. above sea-level, which forms the eastern side of the island of Noss. The cliffs of Noss (Fig. 1) can be divided topographically into three parts, the North (A) and South (B) faces of the Noup, and Rumble Wick (C), the cliff between the Noup and Geordie's Holes, a point above the Holm of Noss. The Holm is a stack on which breeds a colony of over 200 pairs of great black-backed gulls (*Larus marinus*).

On (C) is an excellent stance from which part of the gannet colony can be closely watched, and which alone gives an uninterrupted view of all the inhabitants of one of the large ledges (X). The whole faces of the cliffs (A), (B) and (C) can be viewed from a distance, (B) from (C), and vice versa, and (A) from a shoulder of cliff, the Point of Heogatoug, north of the Noup.

[1] Gannet Population Studies, No. 5.

3. 1937 Estimate and 1938 Count

1937. We visited Noss on 27 and 29 August 1937, before any young gannets had left the nest. On 27 we made a trial, and on 29 a final estimate of the numbers of breeding pairs by the alighting method (**32**).

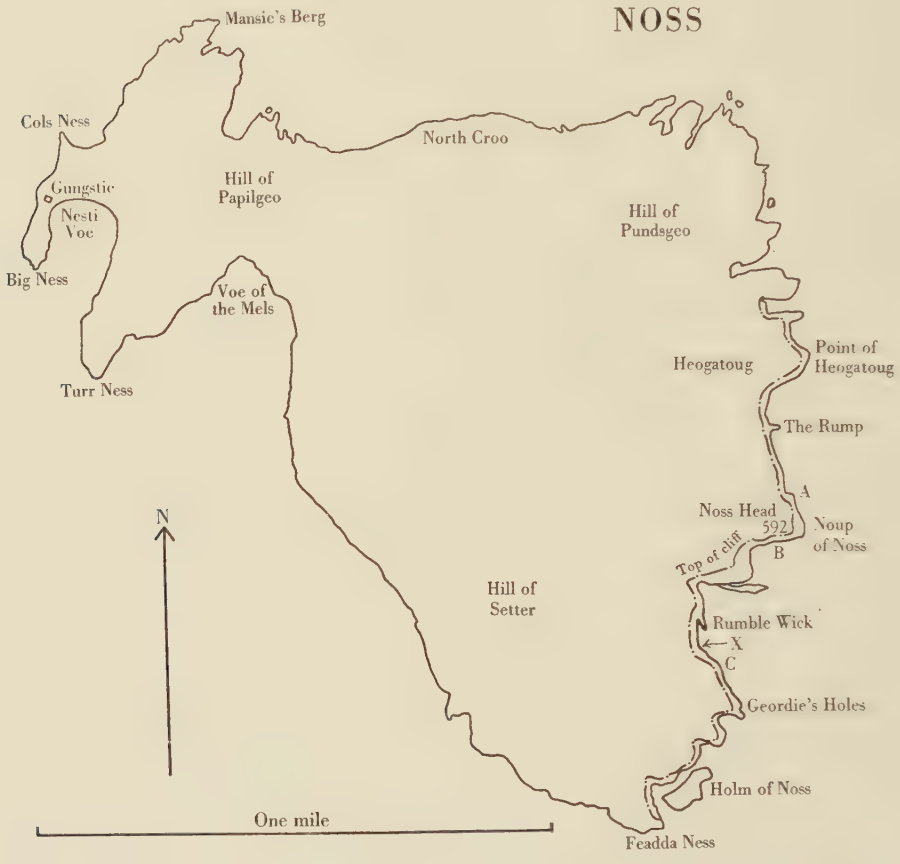

Fig. 1. Sketch-map of Noss, Shetland. (Based upon the Ordnance Survey map with the sanction of the Controller of H.M. Stationery Office.)

We decided to use the ledge (X) as our control group. Five separate counts (by three observers, D. Lack, J. F. and L. S. V. V.) of the number of pairs gave 67, 67, 68, 69, 69: mean 68.

29 August was a calm day and throughout the afternoon there was no change of wind. We first counted the number of birds that alighted on (X) in 30 min., then on (A), (B) and (C) separately in 10 min., then on (X) for a

Phot. 1. The Noup of Noss, from Rumble Wick. *Photo J. Fisher*

Phot. 2. Part of the control area X in June 1935. *Photo L. S. V. Venables*

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Face p. 306

further 30 min. thus tending to correct any change in activity of the whole colony over the intervening period. Our results were:

On (X)	46	alighted in	30	min.
(A)	111	,,	10	,,
(B)	53	,,	10	,,
(C)	71	,,	10	,,
(X)	59	,,	30	,, (2nd count)

i.e. total alighting on (A), (B) and (C) in 10 min. = 235, and mean alighting on (X) in 10 min. = 17·5, which gives as an estimate for the total number of breeding pairs $68 \times 235/17{\cdot}5 = 913$ (to nearest pair).

We cannot claim very great accuracy for this method. Vevers & Fisher (**32**) claimed great accuracy in their original description of the method as used on Ailsa Craig. But as they remark elsewhere (**33**), further studies have meant a revision of their claims, and the figure 913 may involve an error of 20% or more.

1938. In this year we were able to devote the days 22 June to 4 July to the gannets, and found that it was possible, with the aid of powerful glasses, to make direct counts of the number of nests. With the kind help of Malcolm Stewart and the co-operation of Mr G. T. Kay, we obtained the following results:

		J. F. 22. vi. 38	J. F. 30. vi. 38	L. S. V. V. 30. vi. 38	M. S. 3. vii. 38	M. S. 4. vii. 38	Total taken as
A. N. face of Noup (from Point of Heogatoug)		463	480	458	438	—	460
Add dead ground, counted from boat		35	—	—	—	—	35
B. S. face of Noup (from Rumble Wick)	Group 1	—	212, 212	221	241	—	222
	2	—	61	63	57	—	60
C. Rumble Wick (from Noup)	Group 1	109	116	120	106	—	113
	2	292	315	295	296	—	300
	3	—	150, 168	145, 156	152*	176	159
	4	—	171	170	137*	165	169
						Total	1518 nests

* Omitted, owing to mist and the presence of a naval boat letting off rockets.

We consider this count to be much more accurate than the 1937 estimate.

4. Relations with other birds

Gannets compete for nesting sites with only one bird, the guillemot, *Uria aalge* (Pontopp.), since the other cliff-breeders do not use broad ledges on Noss. Guillemots still try to return to the ledges which the growing numbers of gannets have colonized. On these ledges the gannets have "beak-range" territories, between which guillemots may succeed in laying their egg. If the egg should roll within beak range of a gannet it can never be recovered by the guillemot, and in June many can be seen abandoned. This factor is probably of some importance in affecting the number of guillemots on a cliff where gannets are increasing.

On Noss 50 pairs of great skuas, *Stercorarius skua skua* (Brunn.), bred in 1932, 67–70 bred in 1934 (**30**). In 1937, according to the estimate of J. W. Jamieson (**17**), the R.S.P.B. watcher, they had again increased and in 1938 L. S. V. V. counted c. 80 pairs. These birds pursue gannets and make them throw up their fish, but it is impossible to say whether they seriously affect the food supply to the young. They have never been seen to kill an adult or young gannet.

5. Mortality of young

On the control ledge (X) 68 pairs of gannets had 57 chicks on 29 August 1937, which could be expected to fly in from one to three weeks. Since the cliffs fall sheer into the sea, and there is no beach of any kind, mortality cannot be examined at the cliff-foot as on Ailsa Craig and other gannetries.

6. Colonization

Obviously the Noss gannetry and its history brings up the question raised by Ingram & Salmon (**16**) over the Grassholm gannetry. The question arises, is the increase of gannets on Noss due entirely to colonization, or can it be accounted for, after the first few years, by the natural increase of the gannet when undisturbed and protected?

What can the natural increase of the gannet be? We must first find out three things: (*a*) the age at which gannets can breed, (*b*) how many years the "average" gannet will continue to breed, and (*c*) the sex ratio.

(*a*) It is generally held that gannets hatched in year n can breed in year $n+4$, though it has been suggested that they can breed in year $n+3$. Gurney (**13**) rather avoided the question in his book. Booth (**6**) is the only man to have bred the gannet in captivity. He obtained from the Bass Rock:

In 1874, 4 fledglings,
In 1875, 2 ,,
In 1876, 2 ,, .

In 1879 a pair began to build, and he states that "after sitting five or six days the *young birds* [our italics] succeeded in dragging away some of the materials and smashed the egg. The nest was reconstructed immediately; but though the bird continued sitting for several days, it was eventually deserted." In 1880 and 1881 the same pair brought young off successfully. It is clear, then, that the pair which tried to breed in 1879 came from the Bass Rock as fledglings in 1874 or 1875, and bred when the 1876 pair were still "young". This points to $n+4$ (or $n+5$) breeding, and provides some evidence for ruling out $n+3$. Booth's study of plumage changes (supported by pictures) also seems to show that full plumage is not attained until at least $n+4$. We are therefore supposing that a gannet hatched in the year n can breed in the year $n+4$.

(*b*) There is very little evidence on the longevity of gannets. Records from captive birds in zoos (**9**, **10**) give us (London) 12 years, 9 months, 27 days; and

6 years, 1 month; (Copenhagen) two birds about 13 years. The mean length of life of the eight longest-lived in captivity, mostly caught as adults, is about $8\frac{1}{2}$ years. On the other hand, the closely related pelicans may live in captivity up to 51 years. Evidence from ringing returns is scanty and cannot yet be expected to give a satisfactory contribution to this problem; with the exception of a private scheme in 1904 (**28**) ringing of gannets has only seriously been carried out since 1913 (**36**). The longest lived ringed gannet recovered so far was marked on Ailsa Craig as a nestling on 30 July 1924 and recovered near the Craig on 1 April 1932 (**3**). Maynard (**22**) dissected a female gannet "with the ovaries nearly depleted, there being about a hundred and forty ruptured capsules, among which are interspersed a comparatively few ovules. As a ruptured capsule indicates most surely that an egg has been deposited, it is reasonable to suppose that this gannet has laid something like one hundred and forty eggs and, as there is but one egg normally laid in a season, this would give an approximate great age to the bird, even if we allow for occasional accident to an egg, when a second specimen would be deposited that season."

(*c*) Gannets appear to be strictly monogamous birds; amongst a mass of negative evidence for this, we must adduce the positive fact of their very rigid type of mutual courtship. Therefore it would be unsafe to say that if there were more females than males, there would be more chicks per gannet. On the contrary, a sex ratio other than 1 : 1 would tend to lower the potential increase. In the absence of any statistical evidence, we are *assuming* that the sex ratio is actually 1 : 1.

The argument that follows is put forward after consultation with Prof. J. B. S. Haldane (**14**), and the writers are very grateful to him for his assistance with this biometric problem. C. F. Fisher has also given useful help.

Suppose there are p_n pairs of gannets in the year n, aged 4 years and over, and that each produces 1 chick, the sex-ratio being 1 : 1. The maximum rate of increase is given if all birds are immortal and perpetually fertile. In this case the number in each year, provided no colonization takes place from outside, is increased by half the number of birds hatched 4 years earlier, i.e. by $\frac{1}{2}p_{n-3}$.

Thus if $n = 1936$, $$p_{1937} = p_{1936} + \tfrac{1}{2}p_{1933}.$$

In general, $$p_{n+1} = p_n + \tfrac{1}{2}p_{n-3},$$

or $$p_{n+4} - p_{n+3} - \tfrac{1}{2}p_n = 0. \qquad \text{.....(1)}$$

Hence, in the long run, values of p_n will tend to a geometrical progression whose common ratio is the largest root of

$$x^4 - x^3 - \tfrac{1}{2} = 0, \text{ i.e. } x = 1{\cdot}25 \text{ (approximately)},$$

and $$p_{n+m} = 1{\cdot}25^m p_n, \text{ or } \log p_{n+m} = \log p_n + m \log 1{\cdot}25.$$

On Grassholm in 1924 (**1**) there were about 2000 pairs of gannets. In 1933 there were about 5500 pairs (**26**). Ingram & Salmon (**16**) calculated that this

increase could be caused by an annual increment of about 10%. The actual annual increase x would be given by the equation

$$\log p_{1933} = 9 \log x + \log p_{1924},$$

i.e.

$$\log 5500 = 9 \log x + \log 2000,$$

and

$$x = 1{\cdot}119 \text{ (approximately)},$$

and the annual increase would be approximately 11·9%.

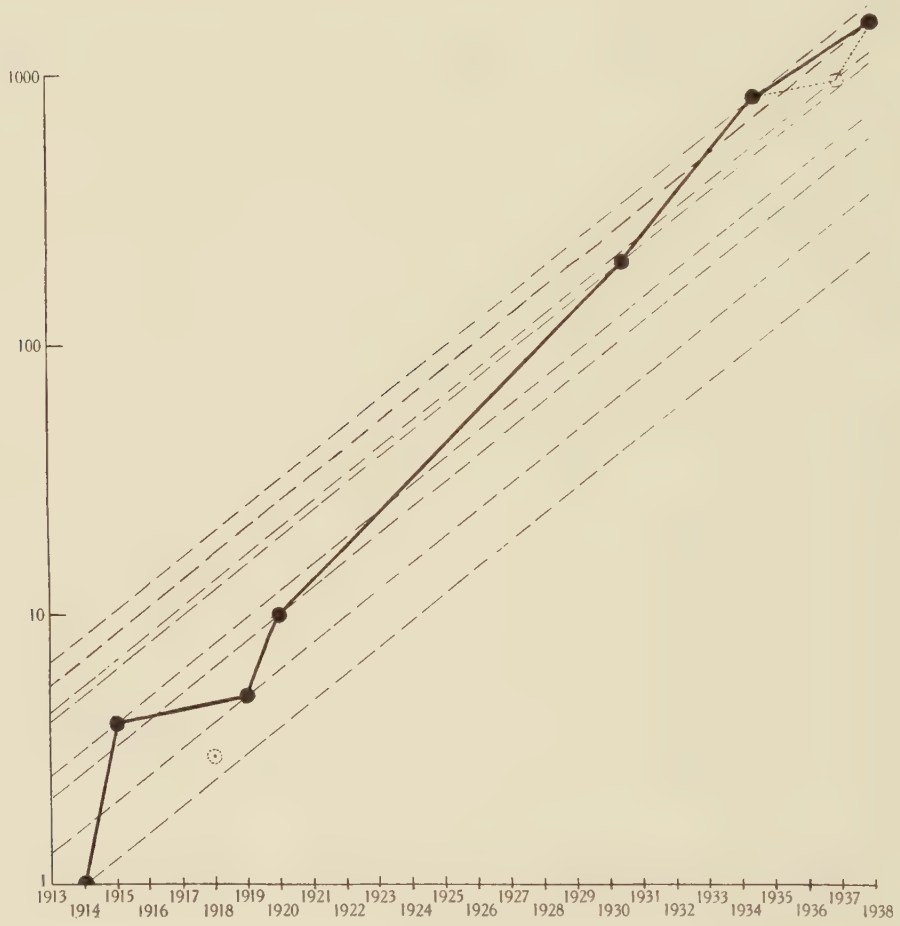

Fig. 2. Increase of gannets on Noss, plotted on arithlog paper. —— actual increase; – – – theoretical increase if there is no colonization, and if all gannets are immortal.

They held, too, that this increase could be accounted for by a survival rate of young equivalent to 30% reaching maturity.

Table 1

Stage of colony	Factors affecting numbers: Promoting	Factors affecting numbers: Limiting
1. Birds interested, and attempts at breeding, e.g. Lundy 1922 (**20**), Isle of May 1922 (**5**), Bempton Cliffs 1924–8 (**24**) and Great Saltee 1929–32 (**23**)	(*a*) Habitat selection Primary, islands Secondary, ledges of right shape and size Tertiary, steep cliff (*b*) General increase in other colonies causing pressure on sites, see (*j*) and emigration	
2. First bird or birds lay eggs. More non-breeders than breeders present, e.g. on Funk Island (**11**), Great Saltee (**23**)	(*c*) Existence of threshold number of birds necessary to provide the required social stimulus to breeding (**5**). A solitary pair can, however, breed, e.g. Horse of Copinsay 1914 (**4**), Noss 1914 (**21**), Great Saltee 1933 (**19**, **23**), and Bempton Cliffs 1937-8 (**6a**)	
3. Colony established and increasing. More breeders than non-breeders	(*d*) Further colonization (*e*) Possibility of greater breeding-efficiency due to social stimulus of increased numbers	
4. Young produced in stage 2, now breeding	(*f*) Element of conservatism now enters. Ringing records show young tend to return to colony of origin. One real exception, bird ringed young Ailsa Craig 19 July 1924 recovered 25 miles N.W. Muckle Flugga, Shetland 9 June 1926 (**2**) (near known colony at Herma Ness)	(*g*) Limits of natural rate of increase (*h*) Mortality 1. In nest 2. In adolescence 3. When adult, which may be due to countless factors including man (**27**, **31**), oiling (**34**), accidents, particularly when landing on cliff, and disease
5. Colony still increasing	(*i*) Plasticity of nest-site selection comes into play. Under pressure from cliff-nesting gannets some will breed on grass and flat ground, e.g. Grassholm (**1**, **26**), which has small cliffs	(*j*) Supply of nest-sites limited (*k*) Quarrying, etc., e.g. Ailsa Craig (**34**), Bull Rock (**13**)
6. Decrease and final extinction. More non-breeders than breeders, e.g. Lundy (**13**)	(*l*) Conservatism so strong that birds will return for many years even if unable to breed, Lundy (**13**) (*m*) Continuance of (*a*)	(*n*) Collectors, e.g. Lundy (**13**) (*o*) Earthquakes, e.g. Grimsey (**15**, **24**) (*p*) Mortality of conservative gannets (*q*) Threshold factor (*c*) now has effect on debit side, but may be overweighed by (*l*) until all is finally lost
7 Recolonization. See (*l*). Examples Funk Island (**11**) after 100 years, Lundy (**20**) attempt after 15	(*r*) See (*a*), etc.	

Supposing, once adult, they were immortal, the actual survival rate y would be given by the equation

$$x^4 - x^3 - \tfrac{1}{2}y = 0,$$

i.e. $$y = 0{\cdot}3334 \text{ (approximately)},$$

and one-third would reach maturity.

7. Conclusions

(*a*) *Special.* We may conclude, from a study of Fig. 2, that the numbers of gannets were small and perhaps unsteady for the first six years, but that afterwards increase took place at a rate greater than is possible in a closed population, even supposing all gannets to be immortal. Colonization from outside has therefore taken place right up to 1934 or 1935. After that it can be seen that the actual rate of increase has fallen below the "immortality rate", and we have no clear evidence for further colonization.

(*b*) *General.* The establishment and history of a colony of sea-birds such as gannets deserves examination in the light of Fraser Darling's recent book (**7**) on bird flocks and the breeding cycle. Let us frame our treatment in the form of Table 1 (p. 311).

8. Summary

1. Gannets (*Sula bassana* L.) on Noss, Shetland, have increased from 1 pair in 1914 to 1518 breeding pairs in 1938.

2. Relations with other birds are discussed.

3. On 29 August 1937 a group of 68 pairs had 57 chicks.

4. Until 1934 or 1935 colonization took place from outside.

5. There is no evidence for colonization after 1935, though it is probable.

6. If gannets were immortal and perpetually fertile, their increase in a closed community would be approximately 25% per annum. In nature, then, an increase more rapid than this *must* be partly due to colonization.

7. If only one-third of young gannets reach maturity, and once mature are immortal, their increase in a closed community will be approximately 12% per annum. In nature an increase more rapid than this is *probably* due to colonization.

8. An increase of under 12% per annum gives no clear evidence for colonization.

9. The effect is discussed of such factors as habitat selection, social breeding stimulus, "conservatism", possible rate of increase, mortality, supply of nest sites, earthquakes, collectors and man on the history and numbers of a gannet colony.

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THE COMPARATIVE BREEDING ECOLOGY OF TWO SPECIES OF *EUPLECTES* (BISHOP BIRDS) IN USAMBARA

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(*With* 2 *Figures in the Text*)

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1. Introduction

Euplectes nigroventris Cassin, the Zanzibar red bishop, and *E.h. hordeacea* (Linn.), the crimson-crowned bishop, are weavers of the subfamily Ploceinae. On the biology of the former species nothing appears to have been recorded hitherto except the notes reproduced by Reichenow (1904) and those of Vaughan (1929), who (rightly) suspected it to be polygamous. For *Euplectes hordeacea* we take the work of Lack (1935) as basis and amplify only certain points. Our study is more incomplete than we should have wished because we could not make continuous observations and because of an unexpected technical difficulty.

The males of both these bishop birds have a highly conspicuous red breeding dress and are at other times practically indistinguishable in the field from females and young. Both are territory-holding species dependent on grasses for their food and their nesting materials. The architecture of their nests, which are similar except in size, demands close upright vegetation. The rather restricted geographical range of *E. nigroventris* is wholly contained in that of *E. hordeacea*. The two species may often be found side by side, but in our experience there is little ecological overlap; the smaller *E. nigroventris*

prefers more swampy conditions than the other bird, and we have not found them both numerous in proximity, although this may occur elsewhere (Fuggles-Couchman *in litt.*). Practically all our observations on *E. nigroventris* have been made at Mkomasi near Buiko, under the western edge of the Usambara Mountains, and those on *E. hordeacea* between Amani and the coast. (For map and general description of the country see Moreau (1935).) Owing to the height of the vegetation in which they usually nest—6–10 ft.—an elevated viewpoint is necessary for working out the territories of both species; of the two, *E. hordeacea* is much the more difficult to obtain nesting data for, because the vegetation it prefers is exceedingly tall, dense and bristly.

Fig. 1. Male and female *Euplectes nigroventris* in amorous flight. N.B. Male is red and glossy black; female dappled.

2. *Euplectes nigroventris*

(*a*) *The environment*

The flood plain occupied by these bishops at Mkomasi traverses *Acacia*-desert-grass country and is dependent, not on the local rainfall of less than 20 in. a year, nearly all falling from March to May, but on the water that comes off the South Paré Mountains. As the locality is only about 1500 ft. above the sea and 5° from the Equator the temperatures are high. Mean standard maxima vary from just under 25° C. in the coldest months, June and July, to 34° C. in the hottest, January and February, and 33° C. in March. The corresponding minima are about 16 and 22° C. The eco-climate in the vegetation inhabited by the nesting bishops undoubtedly differs from that of the "standard climate", but the nature and extent of the difference depends on the type of vegetation and the height at which the nests are built (cf. Geiger, 1927; Normand, 1938).

The biological low ebb in the flood plain is from the beginning of August onwards, when the dry season has already lasted some weeks. Except for the perennial water plants, bulrushes and reeds (*Phragmites mauritianus*),[1] the vegetation is all withered and "laid"; none of the *Euplectes* or other weavers are breeding, although they are present in innumerable flocks out of plumage and are still able to find plenty of fallen seed to live on. In some years, but not all, the desiccation is progressive, with increasing heat, until the "long rains" break in March; and annually during this period the weaver birds, including the *Euplectes*, always gradually disappear to some unknown destination.

If the "short rains" of October to December are exceptionally heavy in the mountains, or even in the event of a single cloudburst there, the riverain strip at Mkomasi becomes more or less flooded and in a short time well supplied with the important food grass, *Echinochloa haploclada*. Very few weaver birds of any species breed during that spell of what appear to be suitable conditions; but every year in March, April and May immense numbers of *Euplectes nigroventris*, *Quelea erythrops*, *Q. aethiopica*, *Ploceus aureoflavus*, *P. bojeri*, *Coliuspasser eques* and *Urobrachya axillaris*, with a few weavers of other species, nest in the rich vegetation of the sodden ground. Whenever the flood plain is wet enough a large proportion of it is put under rice.

The *Coliuspasser* and *Urobrachya* occupy very extensive territories, often superimposed on those of *Euplectes nigroventris* with the minimum of mutual interference. The Queleas breed in seething masses that break down even the bulrushes, and though the bishops do not altogether avoid their neighbourhood it would be impossible for effective territory to be extended over one of these "ecological slums". The *Ploceus* spp. breed in specific colonies of a score or two of nests, the site of which may be wholly within bishop territories. Since these golden weavers are active, noisy, blundering and much more robust than the bishops, one would have expected the latter to avoid their proximity. A cock bishop can chase away a female *Ploceus* that comes too near one of his nests, but although he may threaten a cock *Ploceus* we have seen the latter drive him nearly down into the water under the nests. Although they seem such riotous neighbours, we have no evidence that the golden weavers do any actual damage to the bishops' nests. They steal material from each other but probably the bishops' grasses are too slender to attract them.

(*b*) *The physical nature of the territories*

The breeding habits of *Euplectes nigroventris* resemble those of *E. hordeacea* described by Lack (1935). The males are polygamous, they "sing", display and patrol their boundaries similarly. They are even more disinclined to perch in trees of any height and they spend their lives within about 15 ft. of the ground. As in *E. hordeacea*, the males build the skeleton of the nest, and their part is

[1] We are indebted to Mr P. J. Greenway for the botanical names used in this paper.

completed very rapidly. At 13.00 hours on one day a male was tying his first cross-strands between two upright *Phragmites* stems; by 17.00 the next day his "net-purse" had taken its final shape. In this stage, when it can be seen through at all angles, it is occupied by a female, who, while laying (usual clutch 3, maximum 4), thickens the sides and the bottom with the flowering heads of grasses. During this stage the males are attentive, greeting their mates when they arrive, often sitting close to them while they work, visiting the nest in their absence, and bringing material—but not adding it to the structure. Thereafter the male's interest wanes; the incubation and care of the young are solely the task of the female, who brings insects as well as seed to the nestlings. The male builds other skeleton nests in his territory and they are occupied in rapid succession.

In the Mkomasi flood plain we have observed territories of the following types and occasionally territories not confined to a single type:

(1) In pure stands of *Phragmites*, territories from 9 sq. yd. (fully functional) up to about 120, containing no seed and the minimum of insects. Some of these territories abut on patches of the food grass *Echinochloa*, others do not; some overlap *Ploceus* colonies, others do not.

(2) In pure stands of bulrushes, which also provide no food, territories varying from 60 to over 1000 sq. yd. Some are very heavily infested with *Quelea* and *Ploceus* colonies; only a few abut on *Echinochloa*; most are surrounded by *Phragmites*, bulrushes or the grass *Sporobolus robustus*, which is not eaten by the bishops. Birds so situated have to fly some distance, crossing other *Euplectes* territories, to get any food.

(3) In a consocies of *Echinochloa* and the shrubby herb *Hygrophila spinosa*. No such territories are smaller than about 200 sq. yd. They contain a great deal of food and are not infested with the colonial weavers, though *Coliuspasser* and *Urobrachya* nest in this consocies. A disadvantage of this vegetation is that it is often destroyed for cultivation.

(4) In a mixture of herbage, largely the grass *Sorghum verticilliflorum*, with *Solanum* sp. or *Cyperus* sp., or some *Echinochloa* and *Hygrophila*. Territory size as in type (3), containing proportionately less food but still ample. Other nesting weavers are not common, but the predatory lark-headed cuckoo, *Centropus superciliosus*, may be present. This type escapes disturbance for cultivation because it is developed too late in the season.

It appears that bishops established in types (3) and (4) habitually feed within their own territories; therefore while nesting they can take no part in the rice-eating that is sometimes charged against this species. The bishops of types (1) and (2), which have to fly out of their territories for all their food, seem to make indiscriminately for *Echinochloa* not in a bishop territory or for rice unguarded by its human owners, but further observations on this point are required.

Territories of types (1), (2) and (3) rarely provide any particular vantage point for the owner, or contain an obviously favourite perch as is usual in a territory of *Euplectes hordeacea*. Clearly, then, these adjuncts are not necessary for *E. nigroventris*, but none the less they are utilized if available. For example, a few *Sorghum* heads that overtopped a predominantly *Echinochloa* territory

were constantly used by the owner; and a male with a small territory in bulrushes spent much time on a palm stump just clear of their edge.

Some of the boundaries, especially in the smallest territories, are most rigidly kept. Birds may be seen climbing up and down reed stems within a foot of one another, making hostile gestures and noises, but never attacking. Continued observation shows that the mutual boundary has been fixed between those two stems which are so close together. Nevertheless invading males are able to carve territories out of others that are already small and already contain nests.

It will be seen that the variety of vegetation occupied for nesting is great; some territories have not a botanical feature in common except the general habit of the growth. There is also very wide variation in the amount of overlapping with, and disturbance from, breeding birds of other species. In size the territories vary from 9 to at least 1000 sq. yd.; there is no connexion between their size and the availability of food either within their boundaries or in proximity; both the largest and the smallest territories we have seen contained no food plant whatever. On the other hand, the territories that are well supplied with food are as a rule of moderate size, often about 250 sq. yd.

At the height of the nesting season there is always suitable ground unoccupied. But territories containing no food and suffering the maximum of disturbance from other species can be found crowded together more closely than territories in areas possessing neither of these disadvantages. For example, bishops had several co-terminous territories averaging 60 sq. yd. in bulrushes infested with *Ploceus*, while 50 yd. away a bed of bulrushes began that in 2000 sq. yd. contained no bishop or other weaver. And territories of 9 and 15 sq. yd. existed in *Phragmites* simultaneously with territories of 500 sq. yd. and more in bulrushes and of 300 sq. yd. in *Echinochloa*.

(*c*) *Specific phenology*

So far as the vegetation is concerned, territories of types (1) and (2) could be established at any time of the year; in type (3) when the water has ceased to stand but the ground is still thoroughly wet; in type (4) not until the ground has dried. Most of the early nests are naturally in types (1) and (2), but we have known a bird stake out a claim in type (4) several weeks before any vegetation in it had grown up sufficiently to hold a nest. Thus, as the breeding season progresses, the area eligible for bishop territories increases, by the addition of patches full of the food grass and free of the golden weavers; but we think that the males already established in sites lacking these advantages do not ordinarily transfer themselves.

In 1935 the vegetation was at its best for the *Euplectes nigroventris* by 23 March, territory was being held and nests were occupied. Breeding was still active on 16 June, and on 13 July a few birds, though with diminished territorial instincts, were still in plumage and with occupied nests.

In 1936 conditions were already good by 9 February. A few males were in plumage and had nests, but the great majority were still only coming into breeding condition. On 8 March some males were still not fully red but the majority were breeding hard. We could not visit the place again that year.

In 1937 small patches of suitable vegetation existed during January and February but no bishops were in plumage. On 20 March ample areas of *Echinochloa* were full grown and in seed; some red males were about but we could find no territories. On 24 April activity was at its height; on 20 June not a single *Euplectes nigroventris* in plumage remained, though in spots the vegetation was at least as favourable for continued nesting as it was at the same date in 1935.

About the end of November 1937, exceptional rains produced what seemed optimum breeding conditions. Large numbers of red *E. nigroventris* appeared, took up territory and by 18 December were building. After 29 December no more rain fell, and on a visit on 15 January we found that the whole breeding impulse had been abortive and territories had been abandoned, although the vegetation was still good and red males were common. Reliable native evidence showed that these conditions continued, but very few birds nested for the next three months. At the beginning of May 1938, a sudden recrudescence of activity must have taken place, because on 15 May we found some dozens of nests with eggs but not one with young. By 10 June very few occupied nests and red males remained.

The foregoing observations, discontinuous as they are, show that the dates when the bulk of the *E. nigroventris* come into plumage and breed, vary from year to year in the same locality; but not in such a way as to take advantage of early plant growth. Regardless of the state of the vegetation, breeding ceases at least a month earlier in some years than others, even when it started late. The effective breeding season of the main population varies in different years from under two months to nearly four. We are at a loss for an explanation. Temperature variation from year to year is unlikely to be significant because in these very low latitudes it rarely exceeds 1·5° C. in any given month.

(*d*) *Reproduction rate and sex proportion*

Though we still lack exact fledging and incubation periods it is certain that the young cannot become self-supporting in less than 6 weeks after the first egg of the clutch is laid. Since the nesting season averages barely 3 months, it appears that however frequently each female lays she could not bring up more than two families, together averaging five young, in a year. The maximum number of active nests we have found at the same time in a single territory is five with eggs or young (and two in building), all within a circle of 5 yd. radius in *Echinochloa*. To find four occupied nests at once in a territory is common. One male at the end of the season (13 July) had, in an area of about 10 sq. yd., one nest with three newly hatched young, one with a single fledgling about to

fly, six used nests and one incomplete. The size of the territory could not be ascertained; the male though still present and red, had ceased to keep his boundaries.

It appears then that a successful male commonly attracts four hens at the same time and that up to eight families may be raised in his territory during the season. If all survived, this would give about twenty progeny to each successful male. We do not know of many possible natural enemies, but since we could not get the full history of any individual nests we have no mortality statistics. Destruction of vegetation by man is probably the most potent local check.

An important point, applicable with equal force to *Euplectes hordeacea*, is that although after the breeding season is well under way each territory contains about four females to one male, very few "landless" red males are seen. Thus in any given breeding population the females outnumber the visible males by four to one at the least. This agrees with our observation in early March, just before the mixed flocks broke up, to the effect that the birds showing some signs of the red male plumage numbered about one-seventh of several feeding flocks counted. This result might be brought about in several ways: (1) By genetical sex disproportion. (2) By differential mortality in the nest. (3) By differential mortality after leaving the nest. (4) With an equal average life-span in the two sexes, by the males either attaining sexual powers later in life than the females or losing them earlier.

Possibility (4) can probably be ruled out; for this cause to be effective unaided the sexual life of the average male could only be about one-quarter as long as that of the average female. Also a consequence would be that during each breeding season three-quarters of the male population would be non-functional. Flocks are not to be seen in the breeding areas but non-breeding males might collect elsewhere; or if they did not flock they usually would be accepted by an observer as females. Against late sexual maturity, it may be recalled that Vaughan (1930) collected a red male with frontal bones still incompletely ossified.

Regarding (3) it can only be said that the conspicuousness of the males does not seem to make them a special butt for predators; we have never seen one taken and we know that with *E. hordeacea* most of the territories repeatedly observed retain their identity, and hence presumably the same owners, throughout the breeding season. As regards possibility (2), in our experience the proportion of broods that number three at a late nestling stage does not appear to be much less than the proportion of clutches with three eggs; but we have no bulk of statistics.

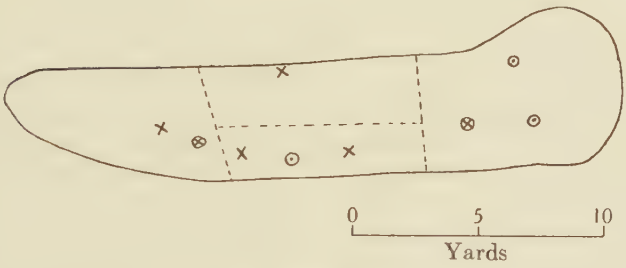
We are left with possibility (1) which, if established, would be of much interest. We accordingly collected about twenty-five nestlings. By the kindness of Mr N. B. Kinnear they were submitted to several zoologists in succession, one of them with special experience in sectioning avian gonads. Our

thanks are due to them for the time they spent on our problem; but to our surprise, and theirs, they all failed to find any evidence, microscopic or macroscopic, of the nestlings' sex. There for the time being this interesting problem rests; but we are attacking it by rearing young taken from the nest.

(*e*) *History of a particular site* (*extreme case*)

A strip of pure *Phragmites* with sharply defined edges has retained its identity in 1935, 1936 and 1937, and its surroundings, on one side a railway bank with some low herbage, on the other almost bare alkaline ground, have not changed. Its area has varied between about 50 and 100 sq. yd., with greatest breadth at any point 5 yd.

A. 4 May 1935



B. 9 March 1936

Fig. 2. Occupation of the same patch of reeds by *Euplectes nigroventris*. × Unoccupied nest, ⊗ nest with eggs; ⊙ nest with young.

On 23 March 1935, when breeding was already general, this *Phragmites* strip was about equally divided between two *Euplectes nigroventris* males, one of which had one new nest and the other two, including one with a female (no eggs). On 4 May 1935 (Fig. 2 A), a third male had established himself, and in territories of 30, 35 and 40 sq. yd. respectively there were (*a*) two nests with eggs and one with young; (*b*) five nests with eggs; (*c*) two nests with eggs and one with young. Later in the month the whole strip was destroyed by human agency. The *Phragmites* soon grew up again and on 9 March 1936, that is, quite early in the season, four males had territories which were rigidly defined, in the space of 70 sq. yd. (Fig. 2 B). It is unfortunate that we were not able to observe further developments.

In 1937 the *Phragmites* was less close and well grown than in the two preceding years. On 20 March 1937, it was unoccupied; on 24 April, one *Euplectes nigroventris* was in undisputed possession of the whole strip, with one skeleton nest and one to which a female was adding; on 20 June the birds were gone and no sign remained of how many nests they might have had.

3. *Euplectes hordeacea*

(*a*) *The environment*

The localities between Amani and the coast at which we have observed this species, including the area studied by Lack (1935), to which we have given special attention, are all at altitudes below 1000 ft. with a fairly well distributed rainfall of 45–60 in. (according to locality). The bulk of this comes with the "long rains" of March to May, and most of the remainder with the "short rains" of October to December, but rainless months at any season are exceptional. The standard temperatures are not quite so high as in the *E. nigroventris* area at Mkomasi, but the yearly course is the same with mean maxima about 33° C. in February and March.

A consequence of the well-distributed rainfall is that suspension of plant growth is not so complete as in the *E. nigroventris* station just discussed. In the highest rainfall area, at the foot of the East Usambara Mountains, which includes Lack's area, the pioneer on ground that has been cleared is the rank harsh grass *Rotboellia exaltata*, the staple food of the nesting *Euplectes hordeacea*, and one that forms dense masses, often in pure stands of a quarter of an acre or more, 10 ft. tall. Its associates are the grasses *Panicum maximum*, also rank-growing and bristly *Sorghum verticilliflorum*. The latter is a favourite nesting site but the former is probably not rigid enough. All these grasses make their chief growth of the year on the "long rains" and seed and wither in the subsequent cool and comparatively dry season. Much new growth takes place on the "short rains", and in spots that have not been cleared *Rotboellia* is ousted by its two associates. Further stages in the succession are the appearance of the mat-grass *Panicum tricocladum*, which the bishops cannot eat or nest in, woody herbs, such as *Vernonia* sp., and bushy growth, a stage in the succession to evergreen forest. Since *Euplectes hordeacea* nests only where there is plenty of tall grass and prefers areas with *Rotboellia*, the same piece of ground does not usually remain equally attractive to this species in successive years.

Other birds that occupy ground attractive to *Euplectes hordeacea* are the very similar *E. capensis*, the much more extensive territories of which overlap those of several *hordeacea* without much mutual interference, and the cut-throat whydah, *Coliuspasser ardens*, a smaller and weaker bird than *Euplectes hordeacea*, but one whose presence seems to cause a certain amount of annoyance. Especially where clumps of *Pennisetum purpureum* are present small

groups of *Ploceus aureoflavus* or *Amblyospiza albifrons* may nest; but the territories of *Euplectes hordeacea* are so much bigger than those of *E. nigroventris* that the presence of such colonial species is of comparatively much less importance.

(*b*) *Specific phenology*

During the off season this bishop is little seen in the areas where it nests and it drifts about the country in dull-plumaged flocks. We have very rarely seen males in the red nuptial dress between mid-October and the end of February inclusive and then only odd ones, apparently not breeding, though they occasionally breed about October in Zanzibar (Vaughan, 1930). Every year a few can be found in full plumage in early March, but it is not until early May, that is in the latter half of the "long rains", that red males are in their maximum abundance. So far as the vegetation and food supply are concerned, we know of no reason why breeding should not take place also in December and January.

In 1934 when Lack (1935)[1] made a detailed study of a nesting area of these bishops, it is not known exactly when the territories he recorded were taken up; but we had found newly hatched young in the district as early as 8 June. Making occasional observations on his territories after he returned to England we found that on 29 September most were still occupied, but one or two of the owners were going out of plumage and were noticeably more tolerant of trespassing males. On 4 October the situation was similar, but by 21 October, when the grass was very dry and brown, not a bishop remained.

In 1935, when we had intended duplicating the observations of 1934, the usual few full-plumaged males were in the district in March, and on 31 March we found a newly begun nest near Tanga. The vegetation in the area including Lack's territories that year was, however, quite different. *Rotboellia* had practically ceased to exist; in territories 2, 4, 5 and 6 the erect *Panicum maximum* was a very strong dominant and in 1, 3 and 7 the mat-grass *P. tricocladum*. Throughout the 1935 season the site of the 1934 territories was unoccupied.

Elsewhere in the vicinity the 1935 season proved to be abnormal. Throughout June, July and August mixed flocks of females and full-plumaged males could be seen moving about and feeding. (In 1934 Lack found mixed congregation only at the drinking-place.) On 4 August we devoted some hours to watching a patch of *Rotboellia* in which three full-plumaged males at first seemed to have established territory; but we soon found that they showed great tolerance of passing males, took no notice of mixed flocks, and on the next day were not in their supposed territories at all.

[1] For purposes of this paper we have been able to refer to a manuscript plan of Lack's, from which he extracted and simplified his published figure.

In fact during the 1935 season we failed to observe any breeding near Lack's area (though we did elsewhere in the Tanga District). On 12 August, four full-plumaged males collected from mixed flocks had testes already deflating; a week later birds in half plumage and with quite small testes were common. Thus in 1935 the phenology was very different from that of the preceding year; the breeding impulse seems to have been locally deficient and breeding plumage disappeared nearly two months earlier.

In 1936 we were away from Africa on leave. In 1937 events followed closely those of 1934 and the vegetation of Lack's main area was similar to what it had been then, with plenty of *Rotboellia*, *Sorghum verticilliflorum* and *Panicum maximum*, but no mat-grass. The area on the north of the road, to which in his figure three territories were shown extending, had, however, made uninterrupted bush growth, so that ground attractive to bishops no longer existed on that side. We can say that territories were established between 15 May and 13 June, though unfortunately illness prevented us from fixing the date more nearly.

As in 1934, the birds seemed to get all their food in their territories and did not visit patches of rice and maize a few hundred yards away. Most of the territories we recorded in June were still intact, with very little alteration of their boundaries, in the middle of August, when no males showed any signs of going out of plumage and nests containing eggs were still common. Thereafter the territories dissolved rapidly. In one group of originally ten only three still held active males on 6 September, and these were abandoned by about 21 September. Three days later a few males were still in the area but they were going out of plumage and had lost their possessiveness. Thus in 1937 the males' activity lasted for between three and four months. It was over nearly a month earlier than in 1934.

On 6 October not a single male was visible; but in a spot that we believe to have been contained in the territory of one of those still present but going out of plumage on 24 September, three females were traced to nests in which they were feeding very small young. The first of the eggs from which these came must almost certainly have been laid about 20 days before, i.e. about 16 September. The inference is that the procreative and the territorial instincts of the male remain active about equally long and fade together—in this instance at the same time as the red plumage begins to go. Also, the females were occupied with a part of their breeding cycle for an appreciable period after the males' had come to an end.

(*c*) *The territories on the same ground in* 1934 *and* 1937

We found that the main conclusions reached by Lack (1935) in 1934 held good in 1937, namely, that the size and the boundaries of the individual *hordeacea* territories have no relation to the amount of the food plant available in each, nor to topographical features. Personally we have so far not seen a

territory that did not consist largely of tall grass; but the composition of the grass occupied varies from practically pure *Rotboellia* to *Panicum maximum* with a little *Sorghum verticilliflorum* or *Cleistachne sorghoides*.

An important general point of difference in the 1937 season was that the boundaries at no time became so rigidly defined as in 1934, when persistent patrollings fixed them within 2 or 3 ft. As a result of the lack of pressure from contiguous owners the boundaries were not as a rule so straight and the territories tended to be irregularly oval rather than rectangular. Correlated with this was the fact that there was more unoccupied interstitial ground, some of which looked to be most eligible.

In the area of about 16,000 sq. yd. taken by Lack the greatest number of territories that could be traced was nine complete ones and part of two others. This gives an average of 1600 sq. yd., compared with 925 in 1934; but owing to the interstices the average area effectively controlled did not exceed 1100 sq. yd. The minimum was about 600 and the maximum not more than 1500.

The combined area of territories II to VI in Lack's plan (1935) held in 1937 only two territories and part of a third. A strip from 10–15 yd. wide bordering the road was not occupied by any birds either in this particular patch or elsewhere in either direction. We can adduce no external reason for this. It seems most likely that occupation in that year was forced nearer the road by the heavier bishop population.

With two exceptions, the ten territories of June 1937 were maintained with hardly any alteration until mid-August, although, as explained, most of the boundaries were not fixed by constant pressure from both sides. The exceptions were contiguous. One of them apparently lost its owner early in July. At the beginning of August the favourite perch of the male in the other territory was taken over by a yellow bishop. At the same time a male *hordeacea* appeared in interstitial ground alongside and began to act territorially, but a few days later was gone.

Other observations we made in 1937 in the same piece of country led us to similar general conclusions; in suitable grassland we found a mosaic of persistent territories usually not much exceeding 1000 sq. yd. but with large interstices. On the other hand in another part of the Tanga District on 2 June 1935 a block of pure *Rotboellia* 80 by 45 yd. (sharply marked off by surrounding native cultivation) was completely divided between six males. Their average territory was thus 600 sq. yd., but one was particularly small, not exceeding 200 sq. yd. Nesting was only just beginning, so it was impossible to say how far the little territory was functional.

To sum up: of about fifty territories worked out, and for the most part repeatedly observed, by Lack and by us, only five covered less than 600 or more than about 1200 sq. yd. In 1937, when the local population pressure was not so great as in 1934, the territories were bigger, but only by about 20 %, when occupation of all the suitable interstices would have increased them by 75 %.

It is a reasonable inference that at least in the Tanga District *Euplectes hordeacea* has a specific territory size of 900 ± 300 sq. yd. irrespective of the specific composition of the grass, provided that it is of the right habit.

4. Comparative Summary

Both *E. nigroventris* and *E. hordeacea* have breeding seasons that are shorter than the vegetation growth would allow. The specific climatic relations are rather different: *E. nigroventris* already has young when the daily maximum temperatures are still nearly at their highest and it continues to breed, through the long "long rains" and on a falling temperature, till the middle of the cool season; *E. hordeacea* breeds at the end of the "long rains" in the coolest months of the year. These specific temperature relations may not be of significance. In Pemba, where the climate is very like that of the East Usambara foothills, Pakenham (1936) found eggs and young of *E. hordeacea* in the hottest months as well as the coolest. Both species vary in the date that breeding condition becomes general and to a striking extent in its effective duration in the same locality in successive years. No reason for the variation can be suggested.

In neither species does the size or the position of the territory bear any relation to the availability of food for adults or young, or to topographical features. *E. hordeacea* territories, however, always in our experience consist largely of grass, while those of *E. nigroventris* may contain none. The great majority of *E. hordeacea* territories occupy 900 ± 300 sq. yd., an area not much affected by abundance of breeding males. Thus in *E. hordeacea* size of territory is possibly specific. *E. nigroventris* on the other hand is almost indefinitely compressible, and moreover its smallest territories are often those with the most obvious disadvantages of lack of food and of crowding by other species. It is probable, in fact, that fully functional *E. nigroventris* territories of under 10 sq. yd. are the extreme examples among those of Passerine birds in which territorial behaviour is developed typically.

Irrespective of the size of his territory a male *E. nigroventris* has up to five breeding females active in it at once and may raise eight families in it during the season. In a territory of *E. hordeacea* not more than three breeding females have been found at once. In the breeding population of both species females outnumber males by quite four to one. We are trying to ascertain whether this difference is genetical.

The foregoing conclusions regarding the territories of the two species are highly relevant to the discussion summarized by Lack (1937). In particular they show that in one species the specific territory size can, on present evidence, be regarded as a limiting factor in population density, while in another, closely allied and with generally similar habits, this possibility is excluded. In the "compressible" species the suggestion of any food motive in the territorial habit can be ruled out with exceptional conclusiveness. Finally, the smallest

territories of the "compressible" species are not obviously less successful than any others of either species.

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AN ECTOPARASITE CENSUS OF SOME COMMON JAVANESE RATS

By GORDON B. THOMPSON

(*With Plate* 14)

Except for my recent paper (Thompson, 1938*a*) containing a census of ectoparasites of the common Ceylon rat (*Rattus rattus kandiyanus* Kelaart) I do not think anything in the nature of a complete census of rat parasites has been published. This paper contains a complete analysis of the ectoparasites collected from 73 specimens of *Rattus rattus diardi* (Jentink) by Dr Felix Kopstein, to whom I am indebted for the opportunity of studying this unique collection. He is to be congratulated on the excellent manner in which he has collected all this material.

Rattus r. diardi is the common Javanese rat and much has been written about it, mostly by Dutch naturalists. It was first recognized as a distinct form by Jentink in 1879, but since that time has been relegated to the status of a subspecies of *Rattus rattus* (i.e. the black rat). Originally described from West Java, it seems to occur commonly throughout the island. According to Tate (1936) "the consensus of opinion is that the species is somewhat variable and about seaports may hybridize with exotics such as *alexandrinus* and *rattus*". In view of these facts it plays an important part in the question of distribution of rat fleas. Dr Kopstein has published three papers (1931, 1932 *a*, *b*) dealing with this aspect of Javanese fleas in relation to plague.

I do not propose to deal with the question of rat fleas and their relation to plague epidemics in this paper but merely to present a detailed table of all the ectoparasites found on specimens of this common rat and to draw attention to certain significant facts presented by the figures. Of the four groups of ectoparasites (ticks, mites, fleas and lice) which one might expect to find on rats, all are represented in the collection under discussion save ticks. I think it can be safely said that we have here a very good representation of the various groups of ectoparasites, except for small mites such as species of *Myobia* which are very minute and difficult to collect on a large scale. All these parasites are blood suckers.

In the accompanying table all the ectoparasites have been counted carefully, and all save the Acarina or mites have been sexed. The mites were far too numerous to permit a count of sexes; the numbers of mites must therefore be taken to include both adults and immatures. In dealing with the fleas I have received a great deal of help from Dr Julius Wagner—the well-known authority on the Siphonaptera. The remainder of the groups have been dealt with for the most part by me.

Of the 73 rats examined, 18 bore lice (i.e. 25 %), 26 bore fleas (i.e. 36 %) and 41 bore mites (i.e. 56 %). (The percentages are only approximate.)

(*a*) *Xenopsylla cheopis*; (*b*) *Stivalius cognatus*; (*c*) *Polyplax spinulosa*; (*d*) *Hoplopleura oenomydis*; (*e*) *Laelaps echidninus*; (*f*) *Liponyssus* sp.

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Those specimens of rats carrying fleas seem to be completely devoid of any other kind of parasite whereas rats carrying lice usually have mites but no fleas. Of the 26 rats carrying fleas 20 were collected at altitudes ranging from 600 to 2100 m., one at 482 m. and five in coastal districts. Rats collected above 1000 m. seem to be more heavily infested than those at lower altitudes. The females of the parasites are very much in excess of the males.

Four species of fleas occur on this rat. The two species of *Xenopsylla* are well known from their association with plague epidemics, *Xenopsylla cheopis* is the commoner species but both the species seem to have a very wide tropical and subtropical distribution with rats as their hosts. Only two specimens of the common cat flea *Ctenocephalides felis* were found. Rats are not the normal hosts of this flea, but owing to rats' association with man's habitations they frequently carry them. The fourth species, *Stivalius cognatus*, is a much larger flea than the others, and belongs to a group, which is very abundant in the Indo-Australian region. It is the commonest species of *Stivalius* occurring in Java and appears to be confined to that island, where it has been recorded as parasitizing at least eight species of the genus *Rattus*, together with a few other closely related hosts.

With regard to the lice, two species, *Polyplax spinulosa* and *Hoplopleura oenomydis*, occur on *Rattus r. diardi*. In a recent paper (Thompson, 1938*b*) I have pointed out the significance of the occurrence of these two species of rat lice and the light which they throw on the distribution of the rats. I do not propose therefore to say any more here regarding them except to urge the need for careful collection of rat lice from the Indo-Australian and Pacific regions. Mites are the most abundant parasites of these rats in Java. *Laelaps echidninus* is the commonest species and is known to occur on rats in various parts of the world. It is particularly abundant in the tropics. Although the numbers given in the table for this species represent the gross number of individuals, an estimate of the sexes was made of a few samples. The percentage of males was found to be very low (i.e. approx. 4 %).

Referring again to the question of the different groups of parasites occurring on individual rats the following table may serve to emphasize the points mentioned previously.

No. of rats	Fleas	Lice	Mites
	24	0	0
	1	0	1
	1	1	0
	0	0	0
	0	12	12
	0	5	0
	0	0	28
	26	18	41

The interesting points are (1) of the 26 rats carrying fleas only two had other parasites, namely one with eight mites and another with one louse; (2) of the 18 rats carrying lice all except six bore mites as well; (3) 28

Table 1.

Ref. no.	Locality, etc.	Siphonaptera: *Xenopsylla cheopis* (Roths.) ♂	♀	*Xenopsylla astia* Roths. ♂	♀	*Stivalius cognatus* J. & R. ♂	♀	Siphunculata: *Hoplopleura oenomydis* Ferris ♂	♀	*Polyplax spinulosa* (Burm.) ♂	♀	Acarina: *Laelaps echidninus* Berlese No. of specs.	No. of specs.	Undetermined species No. of specs.	No. of specs.
1	North Coast, Tegal, Dec. 1934	.	.	.	.	.	.	.	.	.	1	×	17	.	3
14	,, ,, ,, Nov. 1934	.	.	.	.	.	.	.	.	.	.	×	57	.	.
15	,, ,, ,, Nov. 1934	.	.	.	.	.	.	.	3	.	.	.	.	.	8
61	,, ,, ,, 26 June 1930	.	.	.	.	.	.	.	1	.	.	.	.	.	3
40	,, ,, Cheribon, Dec. 1930	.	.	.	.	.	.	.	.	18	5	.	.	.	9
43	,, ,, ,, Weroe, 6 Aug. 1931	.	.	.	.	.	.	.	.	.	.	.	.	.	.
68	,, ,, ,, 6 Aug. 1931	.	.	.	.	.	.	.	.	.	.	.	.	.	.
72	,, ,, nr. Cheribon, Soeranengala, 9 May 1930	.	.	.	.	.	.	.	.	1	.	.	4	.	8
67	,, ,, Semarang, Oct. 1930	.	.	.	.	.	.	.	.	.	.	.	111	.	3
74	,, ,, nr. Indramajoe, Pabean Ilir, 27 Jan. 1932	.	1	.	.	.	.	.	.	.	.	.	8	.	9
25	East Coast, Banjoewangi, 25 July 1930	1	3	1	5	3	.	.	.	.	.	.	.	.	.
55	,, ,, ,, 23 July 1930	3	1	5	3	.	.	.	.	.	.	.	.	.	.
77	,, ,, ,, 22 July 1930	.	.	1	2	.	.	.	.	.	.	.	6	.	.
82	East Java, Tosari, 1800 m., 20 Sept. 1930	2	.	.	.	.	.	.	.	.	.	.	.	.	.
84	East Coast, Soerabaja, Sept. 1931	15	10	.	.	.	.	.	.	.	.	.	.	.	.
107	,, ,, ,, Sept. 1931	18	16*	.	.	.	.	.	.	.	.	.	.	.	.
3	Mid-Java, Temanggoeng, 583 m., May 1933	.	.	.	.	.	.	.	.	4	.	.	9	.	4
4	,, ,, ,, 583 m., May 1933	.	.	.	.	.	.	.	1	.	5	1	58	.	10
6	,, ,, ,, 583 m., May 1933	.	.	.	.	.	.	.	.	.	.	×	×	.	.
12	,, ,, ,, Kablockan, 630 m., April 1933	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	,, ,, ,, 630 m., April 1933	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	,, ,, Kranggar, 482 m., Oct. 1933	.	3	.	3	.	.	.	.	.	.	.	34	.	.
11	,, ,, ,, 482 m., Oct. 1933	.	.	.	.	.	.	.	.	.	.	.	48	.	.
83	,, ,, Diëng Koelon, 2100 m., 8 July 1931	1	.	.	.	.	.	.	.	.	.	.	27	.	.
106	,, nr. Wonosobo, Kedjadjar, 1427 m., 11 July 1931	.	.	.	.	2	4	.	.	.	.	.	.	.	.
20	West Java, Lembang, 1250 m., May 1931	3	1	.	.	5	5	.	.	.	.	.	.	.	.
31	,, ,, ,, 1250 m., May 1932	.	.	.	.	.	.	.	.	.	.	.	.	.	.
36	,, ,, ,, 1250 m., May 1931	.	.	.	.	.	.	.	.	.	.	.	.	.	.
51	,, ,, ,, 1250 m., Oct. 1932	.	.	.	.	.	.	.	.	.	.	.	.	.	.
69	,, ,, ,, 1250 m., Oct. 1932	.	.	.	.	3	4	.	.	.	.	.	.	.	.

28	West Java, nr. Lembang, Tjiboeriah, 1200 m., June 1932														124	.
76	,,	,,	,,	Tjikole, 1200 m., June 1932	60	55	.	.	1	2	.	.	.	.	.	.
87	,,	,,	,,	Tjiboeriah, 1200 m., June 1932	.	.	.	.	9	14	.	.	.	.	.	.
88	,,	,,	,,	Tjikidang, 1300 m., May 1932	196	125	.	.	7	3	.	.	1	.	.	.
22	,,	,,	Bandoeng, 750 m., June 1932		.	.	.	.	.	.	1	.	6	.	.	.
30	,,	,,	,,	700 m., June 1932	.	.	.	.	.	.	.	.	.	.	4	.
32	,,	,,	,,	700 m., July 1932	.	.	.	.	.	.	5	.	12	1	580	.
34	,,	,,	,,	700 m., June 1932	.	.	.	.	.	.	1	.	1	.	60	12
45	,,	,,	,,	700 m., June 1932	.	.	.	.	.	.	24	9	58	9	62	4
53	,,	,,	,,	700 m., Aug. 1932	.	.	.	.	.	.	45	3	7	1	390	.
57	,,	,,	,,	700 m., Sept. 1932	.	.	.	.	.	.	110	10	42	6	200	.
102	,,	,,	Bandoeng, 700 m., Mar. 1930		.	.	.	.	.	.	.	.	.	.	.	.
46	,,	,,	nr. Bandoeng, Tandjoeng Sari, 854 m., July 1932		.	.	.	.	.	.	.	.	.	.	36	.
49	,,	,,	,,	,, 700 m., July 1932	.	.	.	.	.	.	.	.	.	.	50	.
58	,,	,,	,,	Artjamanik, 1070 m., 1 June 1930	.	.	.	.	.	.	.	.	.	.	3	.
99	,,	,,	,,	,, 1070 m., 1 June 1930	12	14	.	.	2	4	.	.	.	.	.	.
7	,,	,,	Tjiwidej, 1100 m., Feb. 1933		.	.	.	.	.	.	.	.	.	.	9	.
8	,,	,,	,,	1100 m., Feb. 1933	.	.	.	.	.	.	.	.	.	.	12	.
9	,,	,,	,,	1100 m., Feb. 1933	.	.	.	.	.	.	.	.	.	.	30	.
81	,,	,,	Soekaboemi, 600 m., Nov. 1931		3	.	.	.	.	2	.	.	.	.	.	.
21	,,	,,	Sindanglaja, Tjipanas, 1100 m., Dec. 1931		35	21	.	.	.	.	.	.	.	.	.	.
27	,,	,,	,,	,, 1100 m., 10 Feb. 1931	.	.	.	.	.	.	.	.	8	.	.	.
80	,,	,,	,,	,, 1100 m., 11 Feb. 1931	9	3	.	.	4	1	.	.	.	.	.	.
86	,,	,,	,,	,, 1100 m., Dec. 1931	.	.	.	.	1	1	.	.	.	.	.	.
93	,,	,,	,,	,, 1100 m., Dec. 1931	1	1	.	.	.	.	.	.	.	.	.	.
94	,,	,,	,,	,, 1100 m., 11 Feb. 1931	.	.	.	.	.	.	.	.	.	.	15	.
26	,,	,,	Soreang, 740 m., Mar. 1932		.	.	.	.	.	.	.	.	.	.	43	.
90	,,	,,	,,	740 m., 27 Feb. 1932	1	.	.	.	.	.	.	.	.	.	.	.
38	,,	,,	Padalarang, 700 m., Sept. 1932		.	.	.	.	.	.	.	.	.	.	44	.
54	,,	,,	,,	700 m., Sept. 1932	.	.	.	.	.	.	1	.	.	.	9	.
63	,,	,,	,,	700 m., 24 Sept. 1932	.†	.	.	.	.	.	.	.	.	.	.	.
64	,,	,,	,,	700 m., Sept. 1932	.	.	.	.	.	.	3	.	.	.	19	2
70	,,	,,	,,	700 m., Sept. 1932	2	2	.	.	.	.	.	.	.	.	.	.
91	,,	,,	,,	700 m., Sept. 1932	1	.	.	.	.	.	.	.	.	.	.	.
29	,,	,,	Mt. Gedeh, Tjibordas, Rarahan, 1350 m., 14 Feb. 1932		.	.	.	.	.	.	.	.	.	.	9	1
85	,,	,,	,,	,, ,, 1350 m., 6 June 1933	10	2	.	.	1	.	.	.	.	.	.	.
95	,,	,,	,,	,, ,, 1350 m., June 1930	1	.	.	.	.	3	.	.	.	.	.	.
98	,,	,,	,,	,, Goenoeng, 1300 m., 8 June 1930	3	2	.	.	13	7	.	.	.	.	8	.
105	,,	,,	Koeningan, 550 m., 26 April 1931		.	.	.	.	.	.	.	.	.	.	13	.
56	,,	,,	coast, Indramajoe, Pabean Ilir, 27 Jan. 1931		.	.	.	.	.	.	.	.	.	.	3	.
71	,,	,,	,,	,, ,, 11 May 1932	.	.	.	.	.	.	3	.	2	.	26	.
60	,,	,,	coast, nr. Cheribon, Soeranengala, 9 May 1930		.	.	.	.	.	.	.	.	.	.	29	1
73	,,	,,	Buitenzorg, 250 m., 21 Aug. 1930		.	.	.	.	.	.	.	.	.	.	15	.

× I am unable to say how many mites were obtained from these rats. It is possible that other species were present besides *L. echidninus* Berlese.

* 1♀, *Ctenocephalides felis* (Bouché).

† 1♂, *Ctenocephalides felis* (Bouché).

rats out of the total of 73 carried mites only. From these facts it may be said that the presence of fleas on a rat indicates an almost complete absence of any other kind of parasite, whereas lice and mites seem to occur together although mites may be present without lice. We know so little of the ecology of these different groups of parasites, taking the host as the ecological unit, that it is almost impossible to draw any conclusions from the facts presented in the present case, but there does seem to be some relationship between the various groups. The large table containing the analysis of the parasites is arranged as far as possible in geographical sequence. This arrangement tends to show a relationship between the habitat and the parasites present on the host. This possibility must not be overlooked when considering the presence or absence of one or more of the parasite groups. It is not yet possible to say whether the presence or absence of one or more of the parasite groups is determined by a habitat factor or by some biotic one on the host. It may be noted here that the fleas spend only their adult life in association with the host, whereas the lice and mites pass their whole existence on the body of the host. The question of antagonism among the parasite groups must also be considered. Little is known regarding this, but in my own experience in the case of birds I have frequently found that the presence of mites in extensive numbers usually indicates an absence of lice. This point is not, however, borne out by the figures in the present case.

For the photographs I am greatly indebted to Dr J. W. Shackle.

Summary

1. A complete census is given of the ectoparasites collected from 73 specimens of the common Javanese rat (*Rattus r. diardi* (Jentink)).

2. 36 % of the rats carried fleas: 25 % carried lice: 56 % carried mites.

3. Rats carrying fleas seldom had any other parasites on them. As a rule, rats carrying lice had mites on them whereas mites were present without either fleas or lice.

4. The presence or absence of one or more of the parasite groups may be determined either by a habitat factor or by some biotic one on the host.

5. Females of the parasite species are far in excess of the number of males.

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SOME OBSERVATIONS ON THE BIOLOGY OF THE TROUT SALMO TRUTTA, IN WINDERMERE

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From the Laboratory of the Freshwater Biological Association, River Cottage, Ambleside, Westmorland

With 2 figures in the Text

I. Introduction and Methods

The observations upon which this paper is based were carried out while working at the laboratory of the Freshwater Biological Association on Windermere between November 1935 and October 1936.

Windermere is 17 km. in length and has a total catchment of 134 sq. km. It is a long, deep lake with a total depth of 64 m. and the intake region is narrow. Below the centre of the lake is a belt of shallow water with numerous islands and to the south the lake narrows. The fish examined in the course of this work were mostly collected in the north of Lake Basin. It is a lake in an intermediate stage of evolution and has the fish fauna typical of such lakes in Britain, Scandinavia and elsewhere, which are characterized by [illegible] Perca fluviatilis and Salmo trutta. A more complete list of the fish occurring in the lake has been given in a previous paper (Allen, 1936).

The water of Windermere is soft and has a pH of about 6·8. Pentzal (1936) has published the results of a number of analyses of the dissolved substances in the water of the lake.

Nearly all the fish examined in the course of the work with which this paper deals were collected with a seine net. This net was 61 m. in length and 3·1 m. in depth. It was so mounted that it hung vertically in the water with the corks at the surface. In use the net was set in a straight line parallel to the shore and about 91 m. from it and was drawn in three or more lengths of rope attached to the ends. The only fish which were at the surface when the net was set and which escaped capture were those which were caught. A few fish caught by angling are also included in this paper but these were few in number and were caught near the surface and near the shore.

It is generally known that trout live in the deep water of the lake away from the shore as well as among the inshore region, and it is probable that there are considerable seasonal variations in the proportions of the trout population which inhabit the two environments. Since the trout dealt with in this

inhabiting the littoral region, certain reservations have to be made in applying the results to the trout population as a whole. This matter will be discussed further in a later part of the paper.

2. Growth and seasonal changes

In order to investigate the growth of the trout in Windermere the scales of all trout caught were examined. From this examination the age of the fish, its size at the end of each year of its life, and the age at which it entered the lake were determined. The technique of age determination from scales is now so well known as not to require description. As regards the calculation from scale measurements of the size of a fish at earlier stages in its life, it is the usual practice to assume that throughout life the ratio between length of scale and length of fish remains constant. In the Salmonidae there is as yet no decisive evidence on this point, although Segerstråle (1933) has shown that, for several other species of fish, the ratio may change as the fish grows.

Table 1. *The length in cm. of trout at the end of each winter, the results obtained from fish of different ages being given separately*

Age of fish in years	1	2	3	4	5	6	7	All fish
No. of fish	16	161	174	54	9	3	3	420
Length after 1 year	8·0	6·1	5·4	5·6	5·9	4·1	5·8	5·8
Length after 2 years	—	15·4	12·4	13·0	12·5	11·0	12·3	13·7
Length after 3 years	—	—	21·7	21·8	20·1	17·7	23·1	21·5
Length after 4 years	—	—	—	28·3	29·6	24·6	31·9	28·5
Length after 5 years	—	—	—	—	35·8	31·5	39·9	35·8
Length after 6 years	—	—	—	—	—	36·9	44·7	40·8
Length after 7 years	—	—	—	—	—	—	48·3	48·3
% of total collection	4	38	41	13	2	1	1	—

Table 1, which has been calculated on the assumption that the ratio remains constant, shows the mean calculated lengths of the trout examined at the end of each year of growth. The results for the trout of different ages are given separately. While the calculated lengths based on fish in their third and subsequent years are in good agreement, the figures obtained from one- and two-year-old fish are considerably higher. A change in the ratio between scale length and fish length during the first two years could produce this effect, but since there are two other causes known to exist which could cause the high figures obtained for fish in their first two years it is at present better to assume that the ratio remains constant. One of these causes is the selective action of the net used. This had a mesh of 2·5 cm. knot to knot, and consequently tended to allow fish under 20 cm. in length to escape. Since most fish do not reach this size until late in their third year, the net would tend to select the larger individuals of the one-year and two-year classes (i.e. fish in their second and third years). Thus the calculated lengths based on fish in these classes will be somewhat too high. The other cause of the high figures given by fish in the first two classes depends on the age and size of the fish at migration and will be referred to again later.

In Fig. 1 the mean calculated lengths for all fish are plotted against age and it will be seen that after an acceleration during the first year the growth curve is almost linear. The curve has been extended backward to meet the length axis at 2 cm., since this is about the size of newly hatched fry. This continued steady growth appears to be typical of neutral or alkaline waters, while in more acid conditions the rate of growth usually falls off sharply after two or three years. As a contrast with the conditions found in Windermere, the following

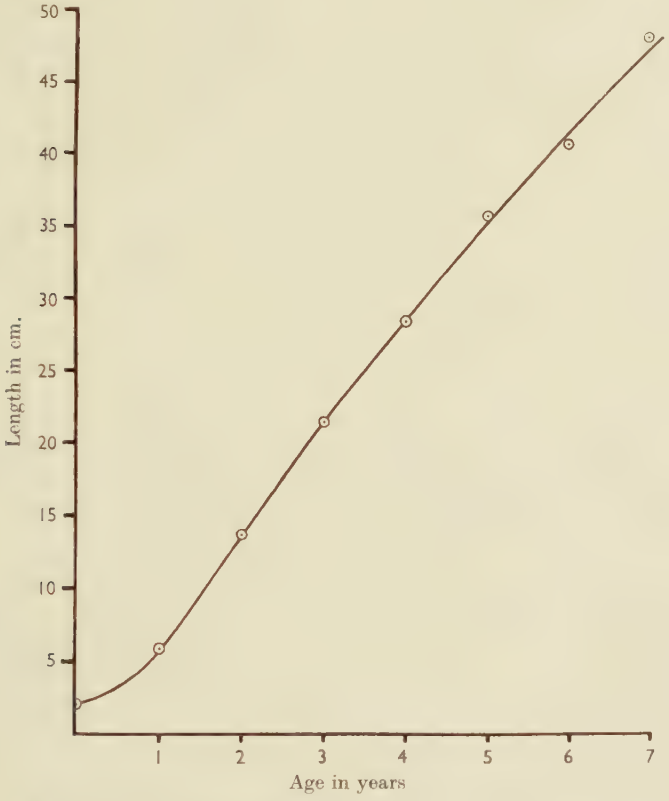

Fig. 1. The mean length of Windermere trout plotted against age.

examples from more peaty lakes may be quoted. In Lough Atorick, a peaty lake in the west of Ireland, Southern (1935) found that while the mean length of the trout after two years was 13·4 cm., after four years it was only 19·7 cm. In Three Dubs Tarn, a small peaty lake near Windermere, it was found that the trout grew to 17·3 cm. in two years, but when four years old were only 23·8 cm. in length. In these two lakes the total growth made during the third and fourth years is only 6·3 and 6·5 cm. respectively, while in Windermere the mean growth over these two years is 14·8 cm.

Observations showed that very few trout under about 12 cm. in length were to be found in the lake, and it was known that the great majority of adult fish entered the tributaries of the lake to spawn. Therefore it was considered probable that the young fish remained in the streams for a few years before descending to the lake. It was decided to examine the scales of the trout to see whether the change from stream life to lake life had any effect on the growth which would appear on the scales. The scales of nearly all fish showed a sudden well-marked increase in the growth rate at some point during the first three years. This effect is almost certainly due to the entry into the lake. Hence it is possible by examining the scales to determine at what age the fish entered the lake. This was done for a sample of 191 fish, and it was found that 12% entered the lake after one year, 76% after two years, and 12% after three years.

Table 2. *The mean growth rates of trout entering the lake at different ages*

	Length in cm. after			
Age at migration	1 year	2 years	3 years	4 years
1 year	7·0	17·7	24·6	33·0
2 years	5·6	13·4	21·6	31·1
3 years	4·4	10·6	18·2	26·0

The mean growth rates of fish which migrated after one, two and three years have been worked out separately and are given in Table 2. The fish which migrated after one year had grown faster during their first year than the others, and those migrating after two years had grown faster during their first two years than those migrating after three years. This effect is well known in salmon and sea-trout.

From this it follows that since all the fish in the one-year class must be first-year migrants, and those in the two-year class must be first- or second-year migrants, these fish should show a higher average growth rate than those in the higher age classes which include the third-year migrants. Also, the fish in the one-year class should show a higher growth rate than those in the two-year class. This, as well as the selective action of the net, will tend to produce the more rapid growth which Table 1 shows to occur in the one- and two-year classes. Since the width of a circulus depends on the rate at which the fish is growing when the circulus is formed, an examination of the circuli at the edge of a scale should show whether the fish was making slow or rapid growth at the time it was caught. If this is done for fish caught at all times of the year it should be possible to determine how far the alternation of slow and rapid growth is a seasonal effect.

Table 3 shows that there is a definite seasonal effect and that in both years 76–100% of the fish are showing rapid growth during the period May to August, while during the winter months the percentage showing rapid growth drops to a low figure. This clearly shows that rapid growth is typically a summer effect; although some fish show rapid growth on their scales during the winter,

probably due to two causes. First, it is possible that there is an overlap between the rapid growth periods of different years, i.e. in some fish the period of slow growth commences early and ends early, while in other fish it only begins late in the winter. Some fish of the first type will have recommenced rapid growth before some of the second type have entered the slow growth period. Consequently, at all times of the year, some fish will be making rapid growth.

Table 3. *The percentage of fish showing rapid growth in each two-month period: also the number of circuli in the outer annulus, the results for wide and narrow circuli being given separately*

	1933	1934					1935				
Time	Nov.–Dec.	Jan.–Feb.	Mar.–Apr.	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	Mar.–Apr.	May–June	July–Aug.	Sept.–Oct.
No. of fish	26	6	35	33	1	9	67	70	66	76	23	26
% showing rapid growth	35	13	51	76	100	0	22	36	61	97	78	54
Mean no. of wide circuli in outer annulus	5·4	3·5	3·9	4·3	5·0	—	12·0	6·1	4·8	7·2	11·0	7·7
Mean no. of narrow circuli in outer annulus	7·2	7·2	6·6	2·1	-	4·9	7·9	9·9	9·7	4·0	4·0	7·8

Close examination of the scales also suggests another explanation. In some fish a wide band of wide circuli is interrupted by one heavy or irregular line. Possibly this means that during the winter the fish made no growth at all and no band of narrow circuli was laid down. If that fish had been captured during the winter and its scales examined, the edge of the scale would have been found to consist of wide circuli. It is, therefore, likely that some at least of the fish found to be showing wide circuli during the winter are of this type.

Table 3 also shows for each two-month period the average number of wide or narrow circuli in each type of outer annulus. For convenience annuli composed of wide and of narrow circuli will be referred to as "wide" and "narrow" annuli respectively. Fig. 2A shows graphically the variation over the period of this investigation in the number of circuli in outer annuli of the "wide" type; while Fig. 2B shows the variation over the same period in the percentage of fish in which the outer annulus is "wide". In both years the maximum number of circuli occurs rather after the maximum percentage of fish with a "wide" outer annulus. This is to be expected since, while the number of rapidly growing fish decreases, those which are still growing rapidly will be adding to the width of their outer annulus, and the mean number of circuli in it will continue to increase.

After the maximum is passed the number of circuli in the "wide" annuli decreases gradually, and not abruptly; and in two cases the decrease begins well before the percentage of slow growing fish has reached its maximum. This

indicates that the fish with wide circuli at the edge of the scale during the winter are not entirely those which have stopped feeding. If this were so the

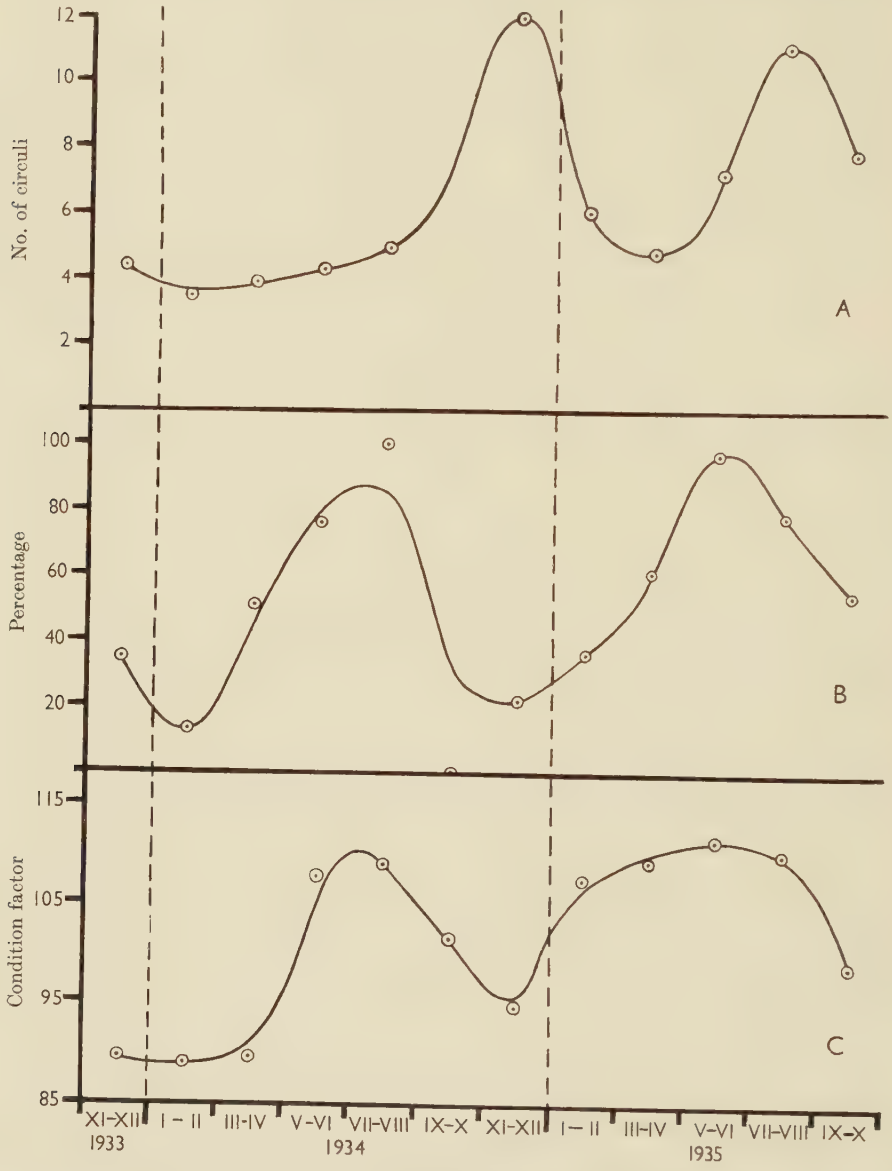

Fig. 2. The following plotted for each two-month period during the investigation. A. The mean number of circuli in "wide" outer annuli. B. The percentage of fish with "wide" outer annuli. C. The condition factor.

width of the annuli of wide circuli in those fish showing rapid growth would remain constant at a high value all through the winter and would fall abruptly

when rapid growth started again in the spring. Similarly, the number of circuli in "narrow" outer annuli reaches a maximum after the percentage of fish with outer annuli of this type has done so (Table 3).

Further information concerning seasonal growth has been obtained by the marking of fish. At various times about 200 trout were captured in the lake, marked and liberated. Before liberating the fish, scale samples were taken from them, and they were weighed and measured. The mark used was a numbered silver label, 9 by 3·5 mm., which was attached by a silver wire to the base of the dorsal fin. If these marked fish were recaptured later they were again measured and, in most cases, a further scale sample was taken. Thus it is possible to determine what has been added to the scales during a known period, and also what growth the fish has actually made during this time.

Excluding fish which were recaptured within three weeks of marking, 32 recaptures have been made, including three fish which were recaptured twice (Table 4). If the increase in length per day is compared with the period during which the fish were under observation, it will be seen that in general the fish which had a period falling largely in the months March to June show a higher rate of growth than the others. For all fish the mean date of the period between marking and recapture has been calculated, and for sixteen fish this date falls in the months February to July, and for the other sixteen in August to January. The mean rate of growth of the first series is 0·0211 cm. per day, while that for the second series is 0·0113 cm. per day. This provides direct evidence, as distinct from that deduced from the scales, that the trout tend to grow faster in the spring and early summer months.

The data about growth made by the scales of the recaptured fish support the view that the alternation between rapid and slow growth shown by the scales of nearly all fish may take place at different times of the year in different individuals. Nos. 112 and 119 were markedwithin a few days of each other and recaptured on the same day, and yet one had added wide circuli and the other a narrow circulus. Also, of the other fish marked in November, 107, 13, 16, 9 added narrow circuli first after they were marked, while 17, 27, 25 added wide circuli first. Comparison of other groups of fish marked at about the same time of year shows other similar cases. This strongly suggests that the overlap theory put forward to account for the wide circuli shown by some fish during the winter may be correct.

It is extremely probable that the same factors which cause a fish to grow fast will also cause it to be in good condition, i.e. its weight will be large in relation to its length. In order to get a numerical value for the condition of a fish, an expression must be used which contains the weight and length and is independent of the size of the fish. The simplest expression of this type would be in the form of W/L^n. If it is assumed that the specific gravity and the shape of the ideal fish remains constant throughout its life, then this expression becomes W/L^3. In the case of some fish, however, there is a progressive change in shape

Table 4. *The history of the marked trout which were recaptured. Lengths in cm.*

No.	Date when marked	Date when recaptured	Length when marked	Increase in length	Increase in length per day	Growth of scales
21	29 Nov. 1933	5 Jan. 1934	24·8	0·6	0·014	No data
101	15 Nov. 1934	15 Jan. 1935	27·4	1·2	0·020	No growth
140	15 Nov. 1934	22 Jan. 1935	22·8	0·6	0·009	No growth
112	23 Nov. 1934	22 Jan. 1935	24·8	1·3	0·022	Two wide circuli
119 (1)	28 Nov. 1934	22 Jan. 1935	21·6	0·6	0·011	One narrow circulus
147	23 Nov. 1934	28 Feb. 1935	28·7	1·2	0·012	No growth
107	15 Nov. 1934	14 Mar. 1935	29·9	1·3	0·011	Two narrow circuli
224	29 Nov. 1935	14 Mar. 1936	22·8	1·4	0·013	No growth
22	25 Nov. 1933	27 Mar. 1934	22·8	1·4	0·011	No growth
17	25 Nov. 1933	27 Mar. 1934	24·2	0·6	0·005	One wide circulus
13	25 Nov. 1933	27 Mar. 1934	22·8	1·9	0·016	Four narrow circuli
27	25 Nov. 1933	27 Mar. 1934	24·2	0·6	0·005	Three wide circuli
16	25 Nov. 1933	8 May 1934	24·2	3·8	0·023	Five narrow and three wide circuli
18	25 Nov. 1933	2 June 1934	26·2	3·1	0·016	No data
25	26 Nov. 1933	3 July 1934	31·2	0·6	0·003	Four wide circuli
9	25 Nov. 1933	9 Dec. 1934	21·6	12·1	0·031	Three narrow, eleven wide, ten narrow circuli
51	25 Jan. 1934	27 Mar. 1934	26·7	0·0	0·000	No growth
165	28 Jan. 1935	17 May 1935	29·3	1·0	0·009	No data
152	22 Jan. 1935	18 May 1935	20·9	2·7	0·023	No data
119 (2)	22 Jan. 1935	23 May 1935	22·2	3·5	0·029	Six wide circuli
185	26 Mar. 1935	25 Apr. 1935	25·4	0·6	0·020	Three narrow circuli
186	26 Mar. 1935	21 May 1935	23·5	1·5	0·027	Six wide circuli
73	27 Mar. 1934	2 June 1934	32·4	0·7	0·010	No data
92 (2)	14 Mar. 1935	18 July 1935	38·2	7·5	0·059	Five wide circuli
195	25 Apr. 1935	27 June 1935	27·5	1·7	0·019	No data
207	23 May 1935	12 June 1935	22·8	0·7	0·035	No data
205	21 May 1935	17 June 1935	25·6	0·2	0·007	No data
100	8 May 1934	10 Jan. 1935	36·3	4·4	0·019	Three narrow, three wide circuli
92 (1)	8 May 1934	14 Mar. 1935	35·7	2·5	0·008	Four wide, four narrow circuli
211 (1)	17 June 1935	18 July 1935	27·7	0·8	0·026	No data
211 (2)	18 July 1935	21 Aug. 1935	28·5	0·5	0·015	No data
269	18 July 1935	19 Sept. 1935	20·4	0·6	0·010	No data

during life so that in order to get an expression for normal condition which is independent of size, values of n must be used which differ slightly from three. The appropriate value of n may be determined for any sample of fish by plotting for each individual fish the logarithm of its weight against the logarithm of its length. If the relation between length and weight is of the type postulated then the points will lie about in a straight line whose gradient is n. This has been done for the trout examined during this investigation, and it has been found that there is no justification for giving n any value other than 3 in the case of Windermere trout.

All the trout which have been caught have been measured and weighed and their condition factor calculated. Measurements being made in centimetres and grams, it is found that the resulting value for the condition factor is in most cases of the order of 0·01. For convenience this figure has been multiplied by

10^4, and therefore the formula used in determining condition is $10^4W/L^3$, and the resulting value is of the order of 100.

Since it was found that there are seasonal changes in the growth rate of the trout, the figures for condition factor were tested for the same effect. The result is shown in Table 5, and is expressed graphically in Fig. 2*c*. Fig. 2 shows that there is a clear correspondence between the average value of the condition factor and the rate at which the fish are growing. Both are at their maximum in summer and at their minimum in winter. Detailed comparison shows that the correspondence is even closer than this. In the winter 1934–5 both condition factor and rate of growth began to increase about the end of November while in the previous winter the increase did not begin until February or March. This suggests that there is a close connexion between condition and rate of growth.

Table 5. *The mean value of the condition factor and its standard deviation for each two-month period*

	No. of fish	Mean condition factor	Standard deviation
Nov.–Dec. 1933	35	89·5	10·4
Jan.–Feb. 1934	11	88·9	8·5
Mar.–April 1934	32	89·5	9·6
May–June 1934	54	107·8	9·7
July–Aug. 1934	18	109·0	9·9
Sept.–Oct. 1934	12	101·5	9·2
Nov.–Dec. 1934	68	94·7	8·3
Jan.–Feb. 1935	66	107·5	12·4
Mar.–April 1935	73	109·2	14·2
May–June 1935	86	111·5	9·0
July–Aug. 1935	24	110·1	7·6
Sept.–Oct. 1935	23	98·9	6·2

One other seasonal change shown by the fish may be considered at this point; this is a change in habitat. As already stated, the fish collected in the course of this investigation were caught in shallow water by means of a seine net. In Table 6 the results obtained with this net during the period 1 November 1934 to 30 October 1935 are tabulated. In the last four months there is a decided decrease in the average number of fish caught in one draw of the net. In the previous year netting was carried out less regularly, but a similar effect was also observed. Since it is unlikely that there was any significant decrease in the efficiency of the netting at this time, these results imply that there were fewer fish in the littoral region of the lake during the period July to October than during the rest of the year. But the trout do not leave the shallows entirely, being approximately one-third as numerous here at this time as they are in the winter and spring months. It is also known from the experience of men fishing for char in the lake that trout are not uncommon in the deep water away from the shore during the whole of the fishing season, March to October inclusive. It appears, therefore, that the trout do not perform a complete migration

between deep and shallow water, such as that made by the perch (Allen, 1935), but that they are at all times distributed between the deep and shallow water, and that there is a seasonal variation in the proportions occupying the two habitats.

Table 6. *The results of netting operations during the last twelve months of the investigation*

	No. of draws made	No. of fish caught	Average no. of fish per draw
Nov. 1934	12	69	5·7
Dec. 1934	3	10	3·3
Jan. 1935	12	58	4·8
Feb. 1935	11	23	2·1
Mar. 1935	16	34	2·1
April 1935	11	27	2·5
May 1935	12	46	3·8
June 1935	15	32	2·1
July 1935	16	18	1·1
Aug. 1935	16	9	0·6
Sept. 1935	10	11	1·1
Oct. 1935	8	9	1·1

Unfortunately it is not yet known whether individual fish move frequently from one habitat to the other, or whether they remain for long periods in either deep or shallow water and only occasionally move from one to the other. Only one trout which was marked in shallow water has been recaptured in deep water, but when it is considered that no netting has been done in deep water, and that angling takes place much more intensively in shallow water than in deep, this cannot be taken to indicate that only a small proportion of marked fish ever move to deep water. Since this particular fish was marked on 22 January 1935, and was recaptured on 18 May 1935, it appears that there is some movement between shallow and deep water at other times than that needed to account for the decrease in the number of trout in the littoral region during late summer. Thus it is probable that there is some interchange of fish between deep and shallow water throughout the year, but there is no evidence at present as to the frequency of this movement by individual fish.

It is not possible, therefore, to determine whether the falling off in growth rate and condition in the late summer is typical of all fish, as it would be if fish are moving frequently between deep water and the littoral region. If, on the other hand, there is only an infrequent movement, the fish captured at this time are those which are now definitely inhabiting the littoral region, and therefore the decreases observed apply only to these fish, and not to the whole population. The fact that there is no marked discontinuity in the growth and condition curves at the time when the fish again become abundant in the littoral region rather suggests that the results are applicable to the population as a whole, and therefore that there is a frequent interchange between deep and shallow water.

3. Food

The nature of the food of a fish is controlled first by what is available and secondly by the behaviour of the fish. The results obtained from the observations on the food of the trout in Windermere may be considered in relation to these two effects. The nature of the food varies very greatly at different times of the year. In Table 7 the percentage which the most important organisms were found to make up of the total food is recorded for each month. The percentage composition of the food varies greatly from month to month, and the year may be divided into three periods, in each of which the food of the trout is composed of a particular type of animal:

(*a*) October–February. During this period trout feed principally upon the permanent bottom fauna, i.e. Molluscs and Crustacea.

(*b*) March–July. During this period the trout feed largely upon the temporary bottom fauna, i.e. insect larvae and pupae. This period merges gradually into the next.

(*c*) May–September. During this period the trout feed largely upon terrestrial insects taken at the surface of the water.

Table 7. *The percentage composition of the food of the trout during each month*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Permanent bottom fauna:												
Asellus	15·1	16·1	1·2	8·4	3·7	—	1·2	—	0·7	1·4	53·7	65·6
Gammarus	70·5	41·2	12·1	8·1	25·3	4·0	0·6	—	10·2	19·4	17·5	29·4
Limnaea	3·9	23·7	7·7	6·4	1·6	0·9	11·2	3·7	3·6	32·7	3·9	—
Total	94·0	83·7	23·3	23·6	30·8	17·7	31·8	4·3	14·9	62·6	77·4	95·7
Temporary bottom fauna:												
Chironomid pupae	—	0·4	53·8	2·0	1·6	—	0·3	0·5	0·2	—	—	—
Nemura nymphs	0·2	2·9	6·0	30·7	3·7	—	—	—	—	—	0·1	0·5
Leptocerus larvae	0·5	0·4	0·8	4·8	15·1	37·1	36·2	—	2·4	2·5	0·3	0·3
Char eggs	—	—	—	—	—	—	—	—	—	—	13·0	—
Total	4·5	14·6	73·8	52·2	22·6	41·4	38·7	2·1	11·4	7·7	20·8	4·3
Surface food:	—	0·7	1·7	21·5	52·5	32·2	25·0	93·1	73·4	1·7	1·5	—

The changes in type of food taken do correspond to changes in the type of food available. The permanent bottom fauna is available throughout the year and is actually most numerous during the winter months (Humphries, 1936). The temporary bottom fauna is numerous during winter and spring, but during the winter most of the individuals are of small size and so this class only forms a suitable source of food during the spring months. Owing to the emergence of insect imagines the temporary bottom fauna is comparatively small during the summer. The third class of food, adult insects, is only available during the summer, but it appears that as soon as it becomes sufficiently numerous the trout feed almost exclusively upon it. That this is so was shown by the fact that in 1935, when, owing to suitable weather, adult insects were numerous from the end of April onwards, trout fed on the surface from this time onwards; while in 1934 surface feeding did not become frequent until the middle of June.

Further, it appears that throughout the summer there is a well-marked daily change between surface feeding and bottom feeding. This is shown by Table 8, which compares the percentage of surface food found in fish caught before and after 7.30 p.m. B.S.T. for each of the summer months. It seems that, with the exception of September when the trout are for a time feeding almost entirely on the surface, the percentage of food taken on the surface is much higher during the day than it is in the evening. Since the number of adult insects which are on the wing and hence liable to fall on the water decreases considerably in the late afternoon and evening, it is very probable that here again it is the quantity of surface food available that determines the type of food taken by the trout.

Table 8. *Comparison of the percentage of surface food in trout caught by day and by night*

	Before 7.30 p.m.		After 7.30 p.m.	
Month	No. of food animals	% caught on surface	No. of food animals	% caught on surface
Apr.	1066	28·1	308	1·6
May	1453	89·4	1964	16·1
June	551	36·6	575	1·7
July	308	25·7	15	6·7
Aug.	173	96·0	11	72·7
Sept. (first half)	183	97·3	356	99·7
Total	3734	80·4	3229	21·5

In the table, results are only given for the first half of September, since during this month the amount of surface feeding decreases very rapidly and it so happened that no fish were caught at night in the second half of the month. Thus, means for the month as a whole would be definitely misleading. As illustrating the rate at which surface feeding decreases during September, it can be stated that the percentage of surface food eaten by the nine fish caught in the second half of this month was only 15·9.

The results suggest that when all classes of food are available the trout will feed on the surface rather than on the bottom, and that, if no surface food is present, they will feed on the temporary bottom fauna rather than on the permanent bottom fauna. Schechtel (1927) has also observed that when surface food is sufficiently abundant, the trout in the Tatrasee feed on it in preference to other kinds.

Table 7 also shows that within these main variations in the type of food, definite seasonal changes also occur in the species of the bottom fauna eaten. The following summarizes the main points:

November–December. The principal food is *Asellus*, with a smaller number of *Gammarus*.

November. Towards the end of this month the char spawn on the shore of the lake, and at this time almost every trout caught in the parts of the lake where the char have been spawning has been found to be feeding almost exclusively on char eggs.

January–February. The number of *Asellus* eaten decreases, and *Gammarus* becomes the principal food, while *Limnaea peregra* becomes of increasing importance towards the end of this period. Whether there are corresponding changes in the fauna does not appear to be known.

March–April. At the end of March or the beginning of April there is a short period during which the imagines of *Endochironomus dispar* emerge in large numbers, and during this time the trout feed freely upon the pupae as they ascend to the surface.

April. The nymphs of *Nemura* form an important food. This is very probably correlated with the large size and increased activity of these nymphs just before hatching.

May–July. The larvae of *Leptocerus* now form the characteristic food. The causes of their prevalence in the food at this time are probably the same as those applying to *Nemura* in the previous month.

July–September. This, as already mentioned, is the period in which the trout feed almost entirely on the surface.

As already noted, it is probable that, particularly during the latter part of the summer, a large proportion of the trout are living not in the littoral region but in deep water away from the shore. Therefore surface food cannot strictly be regarded as the typical food of the trout at this time, although it is almost the sole food of those fish which are in the littoral region. Very few fish have been obtained from deep water, but those which have have been found to be feeding on the Crustacea of the plankton and on chironomid pupae. It is probable that the latter were taken as they rose to the surface to hatch.

The figures in Table 7 suggest that the percentages which the most important food animals make up of the food are probably very much greater than are their percentages in the fauna at the same time, i.e. that the fish are performing a definite selection in their feeding. In order to investigate this effect further it was decided to assume that all fish which contained more than 60% of one food animal were selecting food. Applying this test to 180 trout, which all contained ten or more food organisms, the results given in Table 9 were obtained. In addition to the 65% which thus appeared to be selecting a further 6% could have been regarded as selecting two food animals. An arbitrary criterion had also to be used to determine which fish had been selecting two animals. This was taken to be the two species together making up at least 90% of the food, and neither species being less than 30%. As it is very

Table 9. *The numbers and percentages of trout selecting different food animals*

	Numbers		Percentages	
Fish not selecting	—	52	—	29
Fish selecting *Gammarus*	33	—	18	—
Fish selecting *Leptocerus*	25	—	14	—
Fish selecting *Limnaea*	14	—	8	—
Fish selecting *Asellus*	13	—	7	—
Fish selecting *Nemura*	7	—	4	—
Fish selecting Char eggs	5	—	3	—
Fish selecting other animals	20	—	11	—
Total fish selecting one animal	—	117	—	65
Total fish selecting two animals	—	11	—	6
Total	—	180	—	100

unlikely that any of the food animals make up anything like 66% of the fauna, it appears from the table that it is very probable that selection does occur. This hypothesis is strengthened by the fact that on several occasions different fish caught at the same time and place were found to be selecting different foods. Southern (1935) records that out of 80 trout from Lough Derg which contained food 59 were found to have been feeding predominantly on one food. The criterion of dominance is not stated.

It has been shown (Allen, 1935) that in another carnivorous fish, the perch (*Perca fluviatilis*), there are changes in the nature of the food with the size of the fish, and this effect has also been described in other species. With perch in Windermere the small fish feed on zooplankton, the medium fish on the bottom fauna, and the large fish upon smaller fish of the same and other species. The data obtained for the trout have also been examined for this effect. It has been found that very few trout feed upon plankton; this is very probably because the majority of fish do not enter the lake until they are too large to find the small organisms composing the plankton a satisfactory diet. (Out of 339 trout stomachs examined only one contained plankton in any quantity.)

As has been seen, the majority of the trout in Windermere are in the insect feeding stage, although a few trout of all sizes have been found to contain small fish (usually minnows). It does appear, however, that the very large trout over 40 cm. in length feed largely on smaller fish. Only five fish of this size were examined, but four of these had been feeding on other fish which were between 7 and 23 cm. in length; while out of 25 fish between 35 and 40 cm. in length, only five had been feeding upon fish, and only one upon fish over 5 cm. in length. Below 35 cm. no trout had been eating fish over 5 cm. in length, and very few had been eating smaller fish. Thus there seems to be a tendency for fish over 40 cm. in length to feed upon other fish (usually 10–15 cm. in length) while trout below 40 cm. rarely eat fish. But as these large fish are very rare, changes of food with size are quantitatively negligible in Windermere trout.

Table 10. *The amount of food found in the stomachs of trout in each month*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Wt. of food as percentage of wt. of fish	0·30	0·13	0·14	0·17	0·26	0·16	0·07	0·12	0·12	0·10	0·26	0·12
Mean no. of animals per fish	94	23	70	35	67	27	10	28	42	26	88	66

Observations have also been made on the amount of food found in the stomachs of the trout (Table 10). This gives for each month the mean dry weight of the food expressed as a percentage of the live weight of the fish, and also the mean number of food animals found in one stomach. Owing to the wide range of individual variation it is doubtful whether there are any significant differences between the figures for different months, although there may be a tendency for the fish taken in the months July to October to contain less

food than those taken in the other months. Since there is probably a considerable increase in the rate of digestion with increase of temperature, as has been shown for other species of fish (Scheuring, 1928), there may actually be an increase in the amount of food eaten during the summer months. This is in accordance with the increase in growth rate already shown to occur at this time.

4. Population

From the data that have been obtained in the course of this work it is possible to make some estimate of the size and composition of the trout population of Windermere. From the recoveries of marked trout it is possible to gain some idea of the efficiency of the seine net used in catching them. It has been found that a large proportion of the fish remain for a considerable time (up to 18 months) in one place. Analysis of the recaptures of these fish shows that if a fish is recaptured at all, it is on the average recaptured in the third subsequent draw made in the place where it was liberated, i.e. the net captures one-third of the trout in the area which it covers. From Table 6 it seems that during the part of the year when the trout are most numerous in shallow water the average catch in one draw of the net is three trout. It follows that the average trout population of the length of shore covered by the net is nine. Since this length of shore is approximately 40 m. and the total shore line of the lake is 40 km., the trout population of the littoral region of the lake is of the order of 9000.

Certain corrections must be applied to this result. Table 1 shows the age composition of the sample of fish examined. Very few one-year-old fish were caught, about equal numbers of two-year-old and three-year-old fish, and rapidly decreasing numbers of fish in later years. Table 1 shows that the average fish does not reach the length of 20 cm. until late in its third year. But the net used allowed some fish under 20 cm. to escape, so that a considerable proportion of the two-year-old fish in the area enclosed by the net would escape through the meshes before the net was drawn on shore; and nearly all the one-year-old fish present would escape in the same way. Therefore the actual percentage which one- and two-year-old fish make up of the total population will be greater than the percentages in Table 1.

When the proportion of fish entering the lake at various ages is considered, and the probable rate of mortality, it appears likely that the actual number of two-year-old fish inhabiting the littoral region of the lake is between one-and-a-half and twice the number of three-year-olds in the same region. The proportion of one-year-old fish, although higher than is indicated by Table 1, is probably still small since the percentage of trout entering the lake as yearlings has been shown to be small. It seems likely that about half the trout population of the littoral region consists of fish in their third year (i.e. fish which have completed two years), about half the remainder are fish in their fourth year,

the rest being distributed between one-year fish, and fish more than four years old.

The estimate previously reached of the total number of fish in the lake was 9000, but, as stated, this did not make any allowance for the one- and two-year-old fish which escaped the net. The three-year-old fish cannot escape through the net and would be estimated accurately. They made up one-third of the sample obtained, and since the figure for the total population reached on this sample was 9000, it is probable that the number of three-year-olds in the lake is about 3000. We have already seen that actually the three-year-olds probably form one-quarter and not one-third of the total population, and therefore it is likely that the total trout population of the littoral region of the lake is of the order of 12,000.

5. Summary

1. The mean annual rate of growth of trout in Windermere remains almost constant throughout life, and is about 7 cm. a year.

2. The majority of the young fish enter the lake from the streams when two years old, although some enter after one and after three years.

3. The fish entering the lake when one year old are larger at the same age than those which migrate later. Similarly those which migrate when two years old are larger at the same age than those which migrate after three years.

4. The percentage of fish growing rapidly, as judged by the width of the circuli at the edge of the scale, is at a maximum (75–100%) in the summer, and at a minimum in winter. Two possible causes of the rapid growth shown by about 25% of the fish in winter are put forward.

5. The condition factor of the fish shows seasonal variations closely parallel to those shown by the percentage of fish growing rapidly.

6. The trout show well-marked seasonal variations in the nature of the food eaten. There are three main periods: in October to February the trout are feeding on the permanent bottom fauna, in March to July on the temporary bottom fauna, and in May to September on the surface food.

7. There is little change in food with the size of the trout, except that fish over 40 cm. in length feed largely on smaller fish.

8. The trout population of the littoral region of Windermere is estimated to be 12,000; of which 50% are fish in their third year, and 25% fish in their fourth year.

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FLUCTUATIONS IN NATURAL POPULATIONS OF COLLEMBOLA AND ACARINA. PART 2

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(*With 6 Figures in the Text*)

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1. Introduction

In a previous paper (Ford, 1937) a quantitative census of Collembola (springtail) and Acarina (mite) populations inhabiting a community of the grass *Bromus erectus* near Headington Wick, Oxford, was reported for the period November 1935 to March 1936. Various censuses of similar populations, made in widely separated districts, showed fluctuations similar to those obtained in the Brometum community. It was suggested that although climatic changes initiated the increases in population density of these forms at the beginning of winter, the subsequent fluctuations could not be entirely accounted for by climate.

The present paper is concerned with a second census of the same community carried out from September 1936 to April 1937 and includes also certain confirmatory observations made in the following winter, 1937–8. A description of the habitat, lists of the species living in it and the techniques used in making counts, have already been given in the paper cited above. This second census has yielded further information on the course taken by the population fluctuations; on the changes, from year to year, in the composition of the community; on the changes, during population fluctuation, of the age distribution

of the springtail, *Pseudachorutes subcrassus* Tbg.; and on the relation between the spatial distribution of the community and population density. That an investigation of the distribution of the community within the habitat might give useful results had been suggested by an examination of some of the results of the first census and a method of sampling was devised to supply this information. Unfortunately, though successful in this direction, this method involved an inaccuracy not discovered till too late for adjustment. However, this inaccuracy was not sufficient to obscure the results and was adjusted in the partial third census of 1937–8. It also proved beneficial in yielding information on the behaviour of individual species which might otherwise have been overlooked.

I am greatly indebted to Prof. G. D. Hale Carpenter who allowed me to continue this work in the Hope Department of Entomology.

2. Sampling methods

It was desired, in addition to obtaining a figure for population density at each sampling date, to get some idea of the evenness, or otherwise, of the distribution of the fauna between the tussocks of *Bromus*. On each sampling date, therefore, nine samples were taken, in three groups of three each, each group being taken from the stock region of a single tussock (region A in Ford, 1937). This permitted measurement of variability both between and within tussocks. Extraction of the fauna was carried out on a battery of small Tullgren funnels and counts were made as formerly described. From 21 September until 23 November 1936 samples were taken at weekly intervals; from then until 21 December at two- or three-day intervals; from 28 December 1936 until 18 March 1937 at three- or four-day intervals; concluding with four sets of samples at weekly intervals in April 1937: in all comprising fifty sets of nine samples each. Throughout this paper population density is expressed as number of organisms per g. of dry grass.

Most estimates of density are somewhat arbitrary from the point of view of the organisms concerned. In this case a more appropriate measure would take into account the area of grass surface available for mite or springtail to walk over. By unfolding the covering layers on the grass stalks, between which these organisms live, we may get a rough estimate of the surface area of a gram of dry grass. Three such estimates were made, giving a mean value of 296 ± 33 sq. cm. per g. of dry grass. The greatest population density recorded in 1936–7 was 45·79 organisms per g. Allowing 0·25 sq. mm. as the area occupied by a stationary organism (a conservative estimate) then at the period of greatest density each individual has territory 2600 times its own area available to it. If in similar fashion, we allow 1 sq. yd. to be the area occupied by a stationary man, then we find that the population of the Brometum, at its greatest density, is rather less crowded than are the inhabitants of Belgium.

Temperature and relative humidity were recorded on instruments kept in a Stevenson screen near the sampling area. Fig. 1 illustrates the general weather record for September 1937 to April 1938. Temperature is based on the records obtained at Headington Wick, the remaining data being obtained from the Radcliffe Observatory, Oxford. It has been demonstrated (Ford, 1937) that the microclimatic conditions affecting the Brometum inhabitants differs considerably from external air climate and the above records are only intended to indicate changes in the latter. A more important index of climatic conditions affecting the Brometum community is obtained in the water content of the grass samples, found by determining the loss of weight taking place during the drying of the samples for extraction of the fauna. This is included in Table 4.

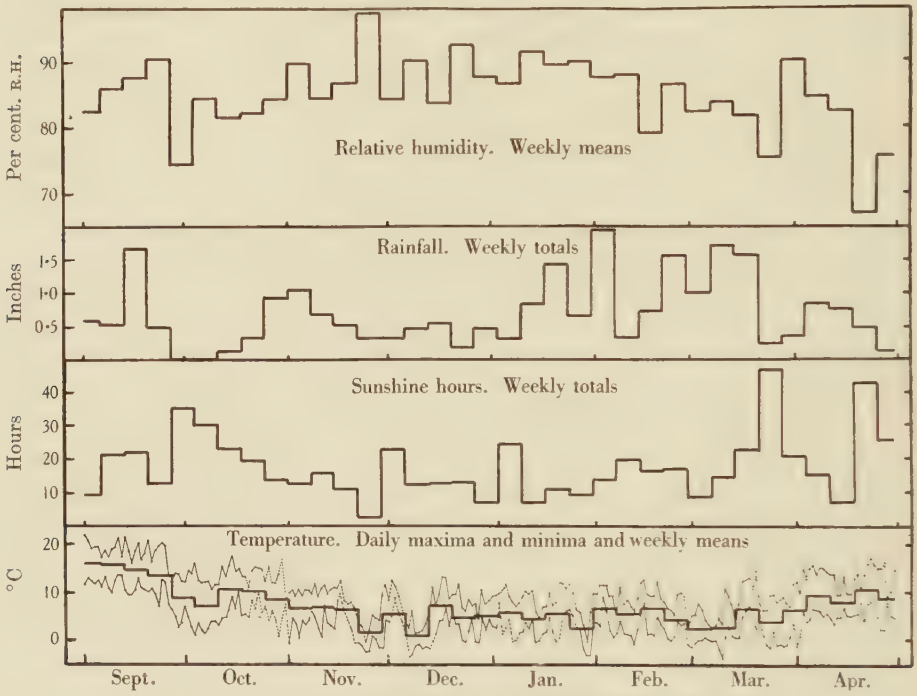

Fig. 1. Climate records, September 1936 to April 1937.

3. Composition of the fauna

Table 1 gives the average densities of the main components of the Brometum fauna in three successive winters, expressed as percentages of the total density.

The principal change was the great decrease in numbers of the springtail, *Pseudachorutes subcrassus*, following the winter of 1935–6.[1] This had the natural

[1] To test the possibility that this species had been affected by the process of sampling carried on in the Brometum, samples, totalling 18·4 g. of dry grass were taken on 8 February 1937, from a patch of *Bromus* which in the first year had yielded a high density of *P. subcrassus* but which had only been sampled twice. Nine individuals were obtained among a population of 601 organisms, thus showing clearly that the decline had been independent of the effects of sampling.

Table 1. *Percentage composition of whole fauna*

	Pseudachorutes subcrassus Tbg.	Other Collembola	*Hypochthonius pallidulus* Koch	*Asca aphidioides* Kram	Immature mites (excluding Trombids)	Trombidiformes	Oribatidae	*Eulaelaps stabularis* Koch	Other Acarina	Thrips	Other species
1935–6	57·5	2·1	8·5	8·6	3·0	5·6	5·3	1·4	1·4	4·7	1·8
1936–7	4·2	3·9	21·0	18·6	20·8	10·7	7·1	7·4	2·5	3·0	0·9
1937–8	0·4	3·9	26·3	6·7	26·8	16·5	4·6	10·2	1·5	2·0	1·1

effect of increasing the proportion of the population occupied by the other two predominant species, the mites *H. pallidulus* and *A. aphidioides*. The second of these species, however, showed a decrease in the third winter. This appears in Table 2, where the percentage composition of the Acarine fauna is shown.

Table 2. *Percentage composition of Acarine fauna*

	H. pallidulus	*A. aphidioides*	Immature mites (excluding Trombids)	Trombidiformes	Oribatidae	*E. stabularis*	Other Acarina
1935–6	25·1	25·3	9·0	16·6	15·7	4·2	4·2
1936–7	23·9	21·2	23·6	12·1	8·1	8·4	2·8
1937–8	28·3	7·3	28·9	17·9	5·0	11·0	1·6

This table, although giving only a partial analysis of the mite fauna, shows that definite alterations had taken place in relative densities of different species. Thus although the small Sarcoptiform species, *H. pallidulus*, continued to reach a high density, the Parasitiform *A. aphidioides* showed a decline; while the third most abundant species, the Parasitiform *E. stabularis* increased. Most notable, however, was the increase, between the first and second winters, of the proportion of immature forms (excluding Trombidiformes).

In addition to the changes in relative density of different species noted above, a marked alteration in the total density of the population of all species took place. An accurate comparison is not possible since the chief results of 1935–6 were obtained by a different technique and expressed according to the number of organisms per unit area. However, during part of that winter samples were also taken according to the present method. Between 24 January and 20 March 1936, parallel sets of samples taken by different techniques yielded average densities of 10,101 organisms per sq. m. and 29·2 per g. of dry grass. The ratio of these figures enables us to compare the population densities of 1935–6 with the two succeeding winters (Table 3). The average density given for 1937–8 is probably too high, as sampling was discontinued in January and thus did not include the whole period of the population decline. This remark applies to any other averages given for this winter later in the paper. Also the average density given for 1936–7 is probably slightly too low, for reasons to be discussed later.

Table 3. *Highest and average densities of the population of all species in three successive winters. (Organisms per g. dry grass)*

	Highest density		Average density	
	Including *P. subcrassus*	Excluding *P. subcrassus*	Including *P. subcrassus*	Excluding *P. subcrassus*
1935–6	85·4	36·3	36·8	15·9
1936–7	45·8	44·7	24·5	23·4
1937–8	44·4	44·1	29·0	28·9

Although it would be rash to postulate any causal connexion between the densities of population of the springtail *P. subcrassus* and the remaining species, Table 3 is certainly suggestive of such a connexion. Although as a result of the almost complete disappearance of this species in 1936–7 the highest density reached and the average density were both lowered, there was an increase in the density of the remaining population (mainly of mites), which was maintained at very nearly the same level in the following year.

4. Data for 1936–7

Table 4 summarizes the data from fifty sets of samples.[1] Each figure expresses the number of organisms per g. of dry grass and is the mean of nine samples. The four principal species are treated separately as above, while other species are grouped under appropriate headings.

In the last column of Table 4 is given the average water content of the samples, expressed as a percentage of their dry weight. From this table the data for population density of mites and for water content are shown graphically in Fig. 2. In this figure and in the table it is seen that their exists a partial correlation between some of the species and the water content of the samples. This is especially so with *H. pallidulus*, and the group of immature mites. With these species the samples showed a higher density when the grass was wet and therefore failed to give a correct value on dry days. It was eventually discovered that this was due to a fault in technique. In 1935–6 the sampling unit used was an area and from this all surface vegetation was removed, including the bases of grass leaves to the level of the roots, which lie from $\frac{1}{8}$ to $\frac{1}{4}$ in. below the soil level. In the smaller (weight) samples now under discussion the grass was cut off at the level of the soil, generally leaving about $\frac{1}{4}$ in. of grass stump untouched. On a previous occasion, when it was thought that the fauna of the grass might have retreated into the soil, examination of the soil had failed to yield any evidence of a downward movement. It was, therefore, necessary in the next winter (1937–8) to determine whether the mites retreated to the extreme base of the leaves during comparatively dry periods or whether the previously undertaken examination of the soil had been faulty.

[1] Space does not permit full publication of results, but a full copy of the original data is being deposited for reference at the Bureau of Animal Population, University Museum, Oxford.

Table 4. *Numbers of organisms per g. of dry grass*, 1936–7, *with percentage water content of samples*

Date	*P. subcrassus*	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites (excluding Trombids)	Trombidiformes	Oribatidae	*E. stabularis*	Remaining Acarina	Thysanoptera	Other species	% water content of samples (mean)
21 Sept.	0·25	1·30	—	6·06	1·32	1·18	2·98	1·10	0·35	1·65	0·23	188
28 Sept.	0·80	0·74	0·03	6·80	6·06	0·62	2·77	0·94	0·40	0·39	0·29	121
5 Oct.	0·44	0·32	—	7·51	6·60	1·01	1·11	0·67	0·31	0·05	0·56	93
12 Oct.	0·36	1·00	0·24	7·68	4·63	1·45	1·61	0·94	0·25	0·19	—	98
19 Oct.	0·61	0·34	0·14	8·47	1·40	2·34	1·31	0·80	0·22	0·59	0·42	84
26 Oct.	0·30	0·38	1·51	4·38	5·90	1·06	1·82	1·14	0·41	0·22	0·27	167
2 Nov.	0·77	0·41	3·18	4·70	11·18	1·17	4·35	1·20	1·96	0·55	0·70	241
9 Nov.	0·60	0·41	1·55	7·63	1·46	4·01	0·66	1·45	0·10	1·38	0·05	112
16 Nov.	1·20	1·21	3·67	4·57	6·65	3·99	1·18	0·60	0·14	0·23	0·08	117
23 Nov.	0·99	0·60	2·06	2·19	3·21	0·90	2·02	1·38	0·50	0·05	0·31	178
25 Nov.	1·05	2·26	11·95	3·45	5·18	5·55	1·43	1·92	0·64	0·57	0·20	163
27 Nov.	1·18	1·24	7·44	7·42	4·67	2·36	1·53	3·02	1·14	—	0·33	181
30 Nov.	2·03	1·19	11·98	6·01	7·19	3·16	1·98	2·95	0·60	1·85	0·60	138
2 Dec.	1·16	2·03	12·07	8·71	8·45	1·73	3·11	1·53	0·68	0·21	0·25	149
4 Dec.	0·75	1·08	6·36	5·61	3·69	3·12	0·35	1·66	0·22	0·33	0·43	88
7 Dec.	2·60	0·36	7·27	4·81	4·01	3·23	1·54	2·09	0·16	0·86	0·10	112
9 Dec.	1·63	0·86	10·26	3·72	3·16	2·56	1·72	1·27	0·75	0·76	0·25	194
11 Dec.	1·05	1·12	26·45	4·55	5·63	2·75	1·35	1·93	0·51	0·34	0·11	200
14 Dec.	1·00	0·61	17·06	4·65	6·32	2·72	1·24	1·96	1·48	0·84	0·38	310
16 Dec.	1·55	0·25	11·78	3·75	7·82	3·11	1·48	3·69	0·88	0·39	0·14	139
18 Dec.	1·96	1·77	6·42	6·49	5·60	5·02	2·36	2·82	0·60	0·59	0·33	180
21 Dec.	1·20	0·56	6·50	4·37	5·27	5·21	0·70	1·63	0·39	0·30	0·09	109
28 Dec.	1·32	0·22	3·21	4·81	7·99	6·86	1·73	2·92	0·28	0·50	0·24	128
31 Dec.	1·50	0·41	4·77	2·64	7·73	4·06	1·26	1·47	0·15	0·95	0·24	93
4 Jan.	2·66	1·35	6·70	4·19	4·59	2·51	1·90	2·33	1·26	0·43	0·43	106
7 Jan.	2·65	0·51	7·51	6·60	5·08	2·88	0·95	1·97	0·41	0·37	0·21	123
11 Jan.	1·71	0·13	6·66	6·06	4·50	2·78	1·40	3·58	0·50	0·60	0·24	130
14 Jan.	1·74	0·84	4·54	5·35	3·59	3·33	2·74	3·19	0·42	0·74	0·22	234
18 Jan.	2·24	2·86	11·69	2·99	15·95	3·35	3·03	1·70	0·73	0·75	—	318
21 Jan.	1·19	1·31	10·78	3·64	5·91	1·60	1·50	0·73	0·69	0·56	0·20	196
25 Jan.	2·06	1·19	3·04	2·99	6·70	2·55	3·19	3·02	0·45	0·59	0·17	230
28 Jan.	1·84	1·03	3·04	4·20	2·66	3·67	1·26	2·52	0·17	1·59	0·13	159
1 Feb.	0·51	1·60	3·08	4·83	3·16	3·87	1·27	2·50	0·14	0·27	0·10	107
4 Feb.	1·47	0·38	2·83	2·81	3·40	4·07	0·94	3·25	0·61	1·38	0·06	270
8 Feb.	1·01	2·93	9·75	2·30	4·10	1·56	2·96	2·92	0·54	1·11	0·16	237
11 Feb.	0·71	0·36	2·84	1·56	4·10	2·88	0·75	1·74	0·20	0·60	0·29	104
15 Feb.	0·93	0·88	1·97	4·02	5·70	3·74	1·42	1·48	0·75	1·25	0·16	143
18 Feb.	0·49	2·00	3·24	2·67	3·93	2·48	2·07	2·86	0·56	1·22	0·11	238
23 Feb.	0·37	0·98	1·94	2·27	4·38	1·93	1·09	1·33	0·81	1·61	0·12	112
25 Feb.	0·30	0·66	4·41	3·83	4·59	1·57	1·54	1·51	1·94	1·00	0·11	296
1 Mar.	0·68	1·36	3·20	5·13	2·15	2·08	0·65	0·72	0·49	1·20	0·37	145
4 Mar.	0·20	0·50	1·45	3·84	4·39	1·16	0·63	1·84	0·64	0·55	0·17	94
8 Mar.	0·49	0·43	1·97	2·65	7·26	2·82	0·93	3·58	0·50	2·16	0·06	174
11 Mar.	0·31	1·04	3·07	3·50	7·95	1·66	1·37	2·20	2·71	0·86	—	174
15 Mar.	0·23	1·20	0·71	3·99	2·59	1·88	1·16	1·38	0·38	1·08	0·23	82
18 Mar.	0·57	1·41	3·52	2·97	1·93	1·42	1·63	1·08	0·27	1·12	0·27	120
1 Apr.	0·19	0·14	0·38	2·05	2·36	0·78	0·89	0·19	0·31	0·86	0·05	86
5 Apr.	0·54	0·46	0·92	4·01	4·01	2·12	2·42	0·55	0·72	0·60	0·22	106
12 Apr.	0·14	0·36	0·19	4·76	2·42	1·53	1·07	0·32	0·35	0·30	0·25	95
19 Apr.	0·18	1·09	1·27	3·66	5·65	1·38	6·30	0·52	0·74	0·26	0·34	164
Means	1·03	0·95	5·13	4·56	5·08	2·61	1·73	1·80	0·61	0·74	0·22	156·5

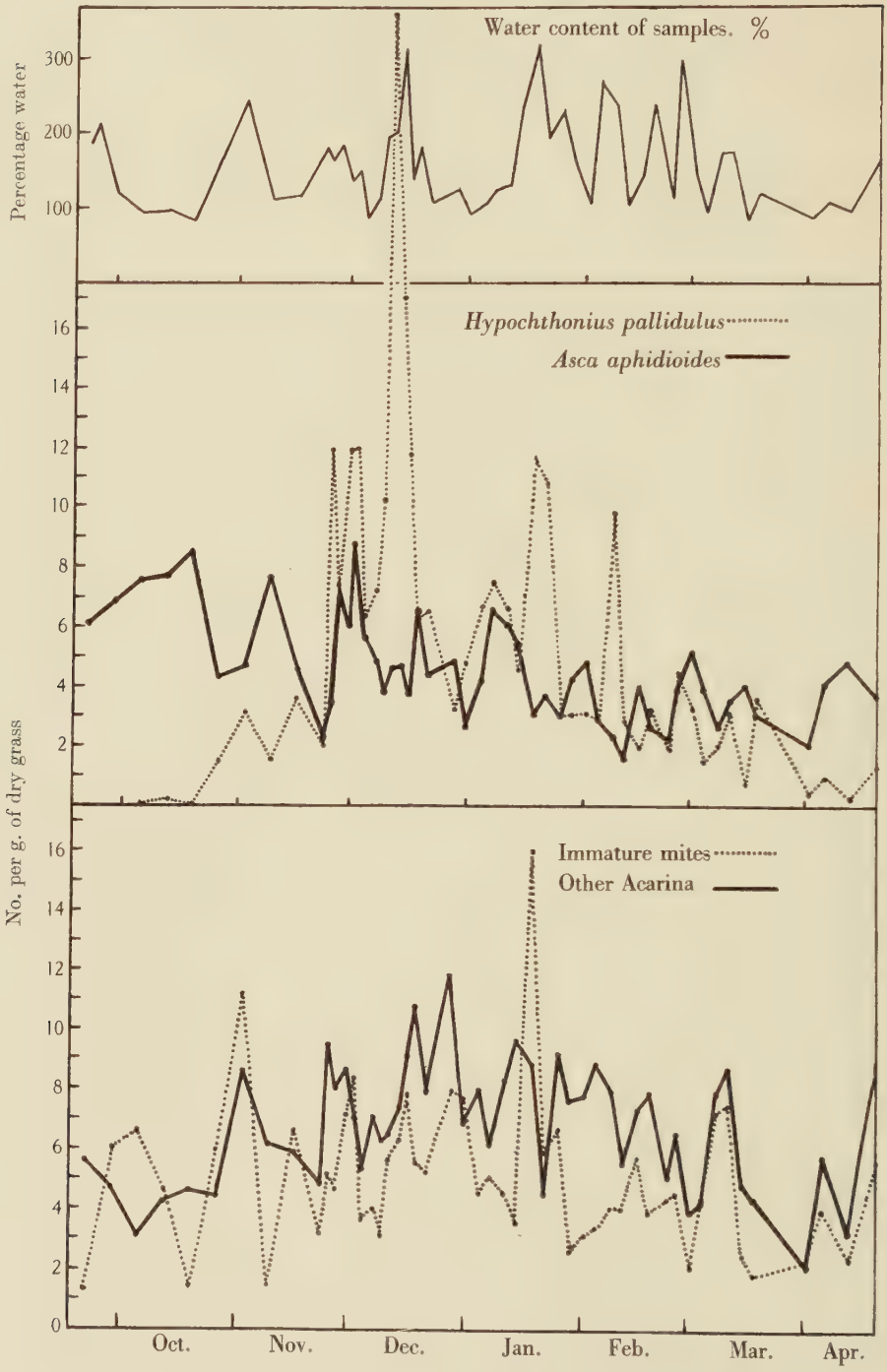

Fig. 2. Density changes in mite population, with water content of samples, 1936–7.

5. DATA FOR 1937–8

Circumstances did not permit frequent sampling in this winter but sufficient data were obtained to settle some of the points at issue in the previous season. Table 5 gives the results of sampling carried out as above, save that individual samples were taken, not in groups of three, but each from separate tussocks.

Table 5. *Number of organisms per g. of dry grass*, 1937–8, *with percentage water content of samples*

Date	*P. subcrassus*	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites	Trombidiformes	Oribatidae	*E. stabularis*	Remaining Acarina	Thrips	Other species	% water content
17 Oct.	—	0·03	0·07	1·92	2·05	3·10	0·18	1·12	0·03	0·24	0·03	—
7 Nov.	0·06	0·26	0·86	1·20	5·30	3·70	2·16	2·90	0·53	0·26	0·20	—
24 Nov.	0·11	1·19	14·26	1·98	8·63	4·35	1·58	3·49	0·29	0·32	0·29	204
1 Dec.	0·07	1·89	6·02	1·99	8·60	3·87	1·86	1·56	0·68	0·59	0·29	222
8 Dec.	0·05	1·80	8·41	2·92	9·48	3·18	1·44	3·18	0·26	0·98	0·31	197
15 Dec.	0·28	2·07	14·82	3·02	11·40	5·15	1·29	4·70	0·73	0·28	0·67	209
21 Dec.	0·23	0·63	9·49	1·71	8·92	6·49	0·91	3·30	0·23	1·02	0·40	260
30 Dec.	0·10	0·73	10·05	2·04	9·32	2·41	1·36	2·78	0·58	0·79	0·21	275
5 Jan.	0·11	1·65	7·35	1·81	7·35	7·39	1·86	4·31	0·58	0·64	0·27	248
13 Jan.	0·05	1·07	8·30	1·26	7·53	5·49	1·36	2·04	0·19	0·19	0·39	198
18 Jan.	0·05	1·07	4·05	1·68	6·93	7·67	0·74	3·25	0·65	1·07	0·60	176
Means	0·11	1·13	7·61	1·96	7·77	4·80	1·34	2·97	0·43	0·58	0·33	221

Some of the data of Table 5 are shown graphically in Fig. 3. On each sampling date it happened that the water content of the grass was high and on no occasion as low as the average for the previous year. The *H. pallidulus* population follows a trend similar to that of the year before, with a peak on 15 December, evidently corresponding to that of 11 December in 1936, though not of so great a density. There is another peak on 24 November which has its counterpart between 25 November and 2 December in the previous year. Whether or not this peak is a true one must remain doubtful, since in 1936 the decline following it was correlated with relative dryness in the samples, though this was not so in 1937. In 1935 a similar decline was detected between 30 November and 29 December (approximately) in the *P. subcrassus* population, but not in that of *H. pallidulus*.

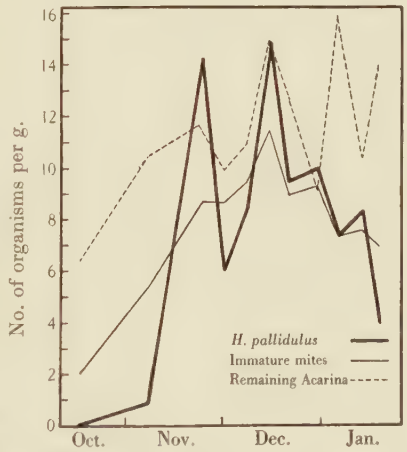

Fig. 3. Density changes in mite population, Oct. 1937–Jan. 1938.

The comparative evenness of the data for the population of immature mites in Fig. 3 may be accounted for by the uniformly high water content of the samples. The combined data for the remaining Acarina (including *A. aphidioides*), however, are irregular and show a tendency to maintain a high density till later in the season, again as in 1936–7.

In addition to the samples treated above, three samples were taken on each date of the leaf bases of the *Bromus*, at ground level. These were extracted as usual and yielded the following results (Table 6).

Table 6. *Number of organisms per g., in leaf bases of* Bromus *at ground level*, 1937–8

Date	*P. subcrassus*	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites	Trombidiformes	Oribatidae	*E. stabularis*	Other Acarina	Thrips	Other species
24 Nov.	—	1·20	0·80	1·60	2·80	—	2·00	—	—	—	0·40
8 Dec.	—	0·65	0·78	1·04	15·20	0·78	1·43	0·39	0·26	—	—
15 Dec.	0·18	3·68	0·88	4·56	11·93	2·10	5·79	1·58	0·70	0·18	0·35
21 Dec.	—	0·65	1·52	2·39	11·75	2·83	3·91	1·30	0·43	—	0·22
30 Dec.	—	1·63	0·41	1·43	12·25	0·20	4·69	0·41	0·61	—	0·82
5 Jan.	—	0·47	0·78	3·44	8·75	1·41	5·15	0·47	0·62	—	0·47
13 Jan.	0·14	1·27	1·13	1·83	5·49	0·84	2·54	0·28	0·42	—	0·56
18 Jan.	0·16	0·66	1·83	2·00	5·33	1·33	3·50	0·16	0·83	—	0·50
Means	0·06	1·27	1·02	2·28	9·19	1·18	3·62	0·57	0·48	0·02	0·41

A third fauna may also be taken into consideration, namely that living in the soil immediately adjacent to the leaf bases of the *Bromus*. In Table 7 the means of Tables 5 and 6 are expressed as percentages and compared with the percentage composition of the surface soil fauna. This latter was obtained by washing out a mixed sample of surface soil, totalling approximately 8 cu. in., collected immediately below the grass samples taken on 24 November 1937 and yielding, in all, ninety-four organisms.

Table 7. *Percentage composition of samples from* (*a*) *grass up to* 2 *in. above soil* (*ordinary samples*), (*b*) *leaf bases of grass at soil surface, and* (*c*) *surface soil*

	P. subcrassus	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites	Trombidiformes	Oribatidae	*E. stabularis*	Other mites	Thrips	Other species
(*a*)	0·4	3·9	26·3	6·7	26·8	16·5	4·6	10·2	1·5	2·0	1·1
(*b*)	0·3	6·3	5·0	11·3	45·8	5·9	18·0	2·8	2·4	0·1	2·0
(*c*)	—	54·3	1·1	—	8·5	3·2	18·1	—	2·1	—	12·8

This table indicates that there exists a distinct vertical zonation in the Brometum fauna and that the soil community is essentially distinct from that inhabiting the grass, the chief link being the Oribatid mites which form approxi-

mately 18% of the soil and leaf base faunas. The 54·3% of Collembola in the soil comprises chiefly a species which does not occur in the grass, *Tullbergia krausbaueri* Born.

This zonation, at least in the grass fauna, is subject to variation with changing climatic conditions. The relative wetness of all the 1937–8 samples does not permit a direct demonstration of this, but the definite positive correlation of *H. pallidulus* density with water content shows that a downward movement of this species and probably certain others (Section 6) to a lesser extent, does occur. It was demonstrated in 1935–6 (Ford, 1937) that on dry days the upper regions of the grass tussocks (not sampled in the present census) were almost devoid of fauna.

6. Movement of species in response to water

We may obtain more precise information on the movement of species in response to water by calculating the coefficients of correlation (r) between population density of the various species and the water content of the samples (Table 4). The results of these calculations are given in Table 8.

Table 8. *Population density of various species and water content of samples. Values for r and P*

	r	P ($n=50$)	
P. subcrassus	+0·181	>0·10	Not significant
H. pallidulus	+0·448	<0·01	Significant
A. aphidioides	−0·249	0·10–0·05	Doubtful
Immature mites	+0·320	0·05–0·02	Fairly significant
Trombidiformes	−0·005	>0·10	Not significant
Oribatidae	+0·266	0·10–0·05	Doubtful
E. stabularis	+0·315	0·05–0·02	Fairly significant
Whole population	+0·437	<0·01	Significant

It is evident from the above table that the mite *H. pallidulus* is strongly affected by the presence of abundant moisture in the grass and it is this species which contributes chiefly to the positive correlation shown by the whole fauna. This being the case, it would appear that a curve drawn through the outstanding points on the curve given in Fig. 2 (i.e. those obtained from samples with high water content), would approach closer to the true state of affairs than that actually shown.

The second most abundant species, *A. aphidioides*, has a doubtful negative correlation and the value for P indicates that the number of samples taken was insufficient to permit of any certainty with regard to this species. It may be noted here that *A. aphidioides* appears to show a periodic fluctuation in density, with intervals of approximately 3 weeks between each peak, from 19 October till 1 February. This is shown in the unsmoothed curve in Fig. 2 and, more clearly, as a smoothed curve, in Fig. 4. A comparison of this curve with that for water content, in Fig. 2, indicates that it is unlikely that the periodicity in

the *A. aphidioides* fluctuations was directly due to the action of moisture on activity of this species.

The positive correlation shown by the group of immature mites (excluding Trombidiformes) is probably a correct one, but it is not possible to come to any definite conclusion with regard to it, owing to the habit of these forms of aggregating to form localized points of very high density. This habit, as much as the correlation of activity with moisture, must be regarded as being the cause of the irregularity in the curve for immature forms (Fig. 2).

7. Fluctuations in population density

Various points about fluctuations were observed, especially in the predominant species, *H. pallidulus*. Commencing at a very low level in October, this species multiplies rapidly and reaches a peak in the middle of December.

Fig. 4. Population trend of *Asca aphidioides*, 1936–7. (Smoothed curve.)

This occurred in each of the three seasons during which observations were made. In the first, however, of 1935–6, the decline following the December peak was followed by another increase, in which the springtail, *P. subcrassus*, also partook. In regard to the first decline, shown in all three seasons, it would appear that the reversal of the population trend is probably due to biotic causes. Table 9 shows some of the climatic averages during the ascent of the population in November and December and during the decline in January and February.

Table 9. *Climatic averages for November–December and January–February* 1936–7

	November–December	January–February
Maximum temperature	7·9° C.	8·5° C.
Minimum temperature	2·1° C.	2·4° C.
Lowest temperature	−3·8° C.	−3·5° C.
Rainfall (total)	4·657 in.	7·992 in.
Water content of samples	157%	188%
Sunshine hours (total)	111·16 hr.	117·55 hr.

There is evidently no significant difference between the temperatures during the two periods, nor in the amount of sunshine. The only feature in which there is a difference is moisture. Here the January–February period is distinctly wetter, and therefore apparently more favourable to the Acarine population than November and December. It would appear from this table that the general climatic conditions of January and February would tend to favour the increase of the population rather than to cause a decline. A further point in favour of a biotic explanation of the reversal of the population trend in December is the similarity in the densities reached at the peak, and the close approximation of the time at which the peak occurred in the three winters. This applies also to the springtail, *P. subcrassus* which, though not abundant in 1936–7, followed a similar trend (see Section 8).

8. AGE DISTRIBUTION OF THE *PSEUDACHORUTES SUBCRASSUS* POPULATION

Metamorphosis does not occur in Collembola and the size of individuals increases at successive moults. Although this increase in size is not necessarily even nor the time between moults equal, we may, nevertheless, obtain figures roughly proportional to age by measuring the length of these insects. With some species at any rate, ecdysis and growth does not cease at maturity (Macnamara, 1919).

During the counting of samples, measurements of all individuals of *P. subcrassus* were made by means of a micrometer eyepiece, from 5 October 1936 to 19 April 1937. Although it transpired that this species was only present in small numbers, a definite increase in population density, culminating in a peak at the beginning of January, was detectable. This is shown as a smoothed curve, derived from the data of Table 4, in Fig. 5. The same figure also shows a similarly smoothed curve for the change in average length of individuals comprising the population (Table 10). The length of these insects varied between 0·20 and 0·75 mm., the mean of 850 measurements being 0·425 mm. By selecting an arbitrary value, in this case 0·40 mm., we may calculate the percentage of the population, at each date, of length greater than this. The smoothed curve so obtained, follows, as might be expected, approximately the same trend as that for the average length. The technique used in sampling is not efficient for procuring the youngest individuals, which are unable to resist the drying process used in extraction. The average length therefore is somewhat less, in reality, than that given above. Similarly, in the consideration of the length (age) classes in the next paragraph, the youngest class, during the period of increase, should have a much greater extension.

There is not sufficient data to enable us to make an accurate division into age classes of the population at each sampling date, but we may summate the age classes in each month. The result of this is shown in Table 11.

Since the sampling methods that were used failed to include the youngest individuals, we may therefore regard the figures of the first column of Table 11 as

Table 10. *Mean length changes in* P. subcrassus *population*

Date	Number measured	Mean length	% over 0·4 mm.	Date	Number measured	Mean length	% over 0·4 mm.
5 Oct.	10	0·49	80·0	11 Jan.	33	0·49	75·7
12 Oct.	7	0·45	71·5	14 Jan.	34	0·46	70·5
19 Oct.	16	0·38	43·8	18 Jan.	30	0·44	56·6
26 Oct.	8	0·34	25·0	21 Jan.	20	0·40	40·0
2 Nov.	30	0·39	43·4	25 Jan.	36	0·48	77·8
9 Nov.	10	0·33	20·0	28 Jan.	22	0·48	63·6
16 Nov.	26	0·37	30·8	1 Feb.	10	0·49	90·0
23 Nov.	16	0·35	31·3	4 Feb.	24	0·43	58·4
25 Nov.	16	0·37	37·5	8 Feb.	13	0·49	84·7
27 Nov.	22	0·37	27·3	11 Feb.	11	0·39	45·5
30 Nov.	40	0·40	45·0	15 Feb.	23	0·49	78·2
2 Dec.	20	0·45	60·0	18 Feb.	10	0·44	50·0
4 Dec.	17	0·35	35·3	23 Feb.	6	0·43	83·4
7 Dec.	48	0·40	41·7	25 Feb.	6	0·45	66·6
9 Dec.	29	0·37	31·0	1 Mar.	10	0·49	80·0
11 Dec.	20	0·43	55·0	4 Mar.	4	0·56	100·0
14 Dec.	21	0·38	33·3	8 Mar.	9	0·49	100·0
16 Dec.	38	0·40	39·5	11 Mar.	8	0·37	37·5
18 Dec.	36	0·38	38·9	15 Mar.	4	0·49	100·0
21 Dec.	23	0·42	43·5	18 Mar.	12	0·40	58·4
28 Dec.	22	0·42	54·5	1 Apr.	4	0·32	0·0
31 Dec.	32	0·39	37·5	5 Apr.	9	0·49	77·8
4 Jan.	56	0·42	48·2	12 Apr.	3	0·34	33·3
7 Jan.	43	0·50	74·4	19 Apr.	3	0·54	100·0

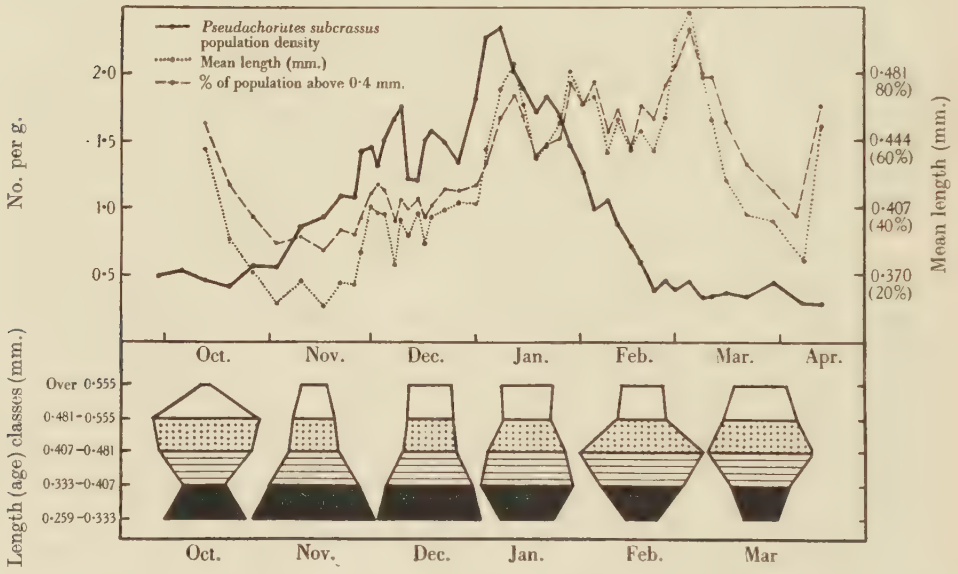

Fig. 5. *Pseudachorutes subcrassus.* Population trend and age distribution.

incomplete. The length (age) distribution diagrams of Fig. 5 are based on the figures from Table 12, in which the data of Table 11 are arranged on a percentage basis after the exclusion of the lowest class, below 0·259 mm.

These results provide a striking confirmation of the existence of a true increase and decline in the population of *P. subcrassus*, in spite of its low

Table 11. *Length (age) classes of* P. subcrassus *each month, October* 1936 *to March* 1937

	Below 0·259 mm.	0·259–0·333	0·333–0·407	0·407–0·481	0·481–0·555	Above 0·555 mm.
Oct.	8	8	4	9	10	1
Nov.	24	51	37	20	17	11
Dec.	36	86	69	43	37	34
Jan.	1	38	65	55	35	36
Feb.	2	10	25	37	15	13
Mar.	3	5	8	14	10	7

Table 12. *Percentage length (age) composition of* P. subcrassus *population*

	0·259–0·333	0·333–0·407	0·407–0·481	0·481–0·555	Above 0·555 mm.
Oct.	25·0	12·5	28·1	31·2	3·1
Nov.	37·5	27·2	14·7	12·5	8·1
Dec.	32·0	25·7	16·0	13·8	12·6
Jan.	16·6	28·4	24·0	15·3	15·7
Feb.	10·0	25·0	37·0	15·0	13·0
Mar.	11·4	18·2	31·8	22·7	15·9

density, for they are precisely what would be expected in such a case. Hitherto age distribution in populations has only received detailed attention in human communities and it is of interest to find that the undercutting of the age pyramid, by the decline in natality during the fall of the population in January and February, finds a parallel in the similar undercutting now taking place in many European countries, which, it is believed, is initiating a decline in the human population. (See, for example, Carr-Saunders, 1936).

Little work has been done on the development of Collembola, save for *Sminthurus viridis* L., a species active during summer, not saprophagous and therefore with little bearing on the present study. However, MacLagan (1932) records for it a life-cycle lasting approximately 50 days, with seven instars, sexual maturity being reached before the completion of the last instar, at about 40 days. Each female may lay up to 100 eggs. *S. viridis* is a much larger animal than *P. subcrassus* and possibly may take longer to reach maturity, but reproduction rates similar to those of *S. viridis* would be sufficient to account for even larger increases in population than were observed for *P. subcrassus* in 1935-6.

9. Distribution of the brometum fauna

It has been mentioned that in 1936–7 samples were grouped in such a way that means for population densities within individual *Bromus* tussocks could be obtained. Three such means were obtained on each sampling date and by use of the standard deviation (σ) formula measures of the variability between tussock means were calculated. Table 13 gives the mean total population densities, of all species (m), with the standard deviation and coefficient of variability $\left(\frac{\sigma 100}{m}\right)$ between tussock means. The data of this table are plotted as

smoothed curves $\left(\frac{a+b+c}{3}, \frac{b+c+d}{3}\right)$ in Fig. 6. Roughly, these curves show that at the beginning of the season, with a low population density, the variability is high; with an increase in the population, the variability decreases simultaneously; at the end of the season, when the population density is again low, the variability once more increases.

Table 13. *Mean total population densities* (m), 1936–7, *with standard deviations* (σ) *and coefficients of variability* $\left(\frac{\sigma 100}{m}\right)$.

Date	Total population (m)	σ	$\frac{\sigma 100}{m}$	Date	Total population (m)	σ	$\frac{\sigma 100}{m}$
21 Sept.	16·42	2·66	16·1	7 Jan.	29·14	7·98	27·4
28 Sept.	19·84	10·71	54·0	11 Jan.	28·16	4·92	17·5
5 Oct.	18·58	7·46	40·1	14 Jan.	26·70	3·56	13·2
12 Oct.	18·35	12·20	66·4	18 Jan.	45·29	13·09	28·9
19 Oct.	16·64	9·42	56·5	21 Jan.	28·11	6·03	21·4
26 Oct.	17·39	5·54	31·8	25 Jan.	25·95	1·37	4·6
2 Nov.	30·17	19·73	64·8	28 Jan.	22·11	3·35	15·1
9 Nov.	19·30	7·13	37·0	1 Feb.	21·33	2·86	13·4
16 Nov.	23·52	9·27	39·4	4 Feb.	21·20	1·95	9·2
23 Nov.	14·21	6·37	44·7	8 Feb.	29·34	9·53	32·4
25 Nov.	34·20	7·95	23·2	11 Feb.	16·03	4·18	27·3
27 Nov.	30·33	0·59	1·9	15 Feb.	22·30	7·67	34·3
30 Nov.	39·54	10·81	27·3	18 Feb.	21·63	2·93	13·5
2 Dec.	39·93	8·93	22·4	23 Feb.	16·83	4·08	24·3
4 Dec.	23·60	7·96	33·7	25 Feb.	21·46	10·14	47·2
7 Dec.	27·03	9·53	35·2	1 Mar.	18·03	8·91	49·4
9 Dec.	26·94	4·85	18·0	4 Mar.	15·37	5·41	35·2
11 Dec.	45·79	8·01	17·5	8 Mar.	22·85	10·76	47·0
14 Dec.	38·26	13·22	34·5	11 Mar.	24·67	16·91	68·4
16 Dec.	34·84	19·81	56·7	15 Mar.	14·83	4·04	27·2
18 Dec.	33·96	15·62	45·9	18 Mar.	16·19	3·60	22·4
21 Dec.	26·22	5·88	22·4	1 Apr.	8·20	2·33	28·3
28 Dec.	30·08	4·76	15·8	5 Apr.	16·57	8·46	56·8
31 Dec.	25·18	7·45	29·5	12 Apr.	11·69	2·24	18·5
4 Jan.	28·35	2·62	9·2	19 Apr.	21·39	9·57	44·6

The following explanation is offered for these observations. It seems evident that the increase of the fauna in October is initiated by a falling temperature and, more especially, by the increase of the moisture in the habitat. (Thompson, 1924, found that the soil population commenced to increase earlier after a very wet summer and autumn.) It is reasonable to suppose that some tussocks, by their density of growth, etc., afford, in unfavourable conditions, better shelter than others for their fauna. These tussocks, therefore, under such conditions, will tend to support a higher population than those not so suitable. This would account for the high variability shown when the population is at a low level. With the amelioration of conditions brought about by approach of winter, more and more tussocks become capable of supporting higher populations and thus there is a decrease in variability between tussock populations and an increase in the total population. When the population again decreases,

variability once more increases, since the population would tend to survive longest in the most favourable tussocks.

That the high variability at the beginning and end of the season is due to the differences between individual tussocks is supported by the increase in-

Fig. 6. Smoothed curves for total population and coefficients of variability, 1936–7.

variability occurring in December immediately following, but not coincident with, the peak of 15 December. It has already been shown that the sharp decline following this peak, from 4 to 28 December is not a true one, but is due to a response by *H. pallidulus*, to drought. We may, therefore, attribute this brief period of high variability to the same cause acting with greater or lesser force in unfavourable and favourable tussocks.

10. Discussion

Before reviewing the results of this community census it is appropriate to discuss briefly the object of community analysis in general, and its relationship to other biological studies. It is generally agreed that the aggregate of organisms of all kinds inhabiting any naturally limited area interact among themselves and with the environment and, in so doing, form a system more or less stable or continuously approaching stability. According to some theories (e.g. Phillips, 1931, 1935) this system is, in fact, an organism: a claim based chiefly on analogies with organisms as commonly understood. It appears preferable, as yet, to refer to organic communities as *ecosystems* (Tansley, 1935) since the nature of the organization characteristic of them has not been critically discussed. The organization of organisms (in the strict sense) has, however, received considerable attention, particularly from Woodger (1929), and, since the kind of organization described by him has great pragmatic value in explaining the status of community studies, it will receive some comment here.

According to Woodger's classification the parts of which an organism is formed stand in a hierarchical relation to one another: the whole organism—organ systems—organs—cells—parts of cells, etc., etc. (This is a simplified version of Woodger's scheme, p. 309, to which it is not possible to do justice in a short space.) The components and the relationships of components in any level of the hierarchy "explain" the entities which form the level above. The whole organism can be "explained" in terms of the nature and relationships of organ systems, these in turn by the nature and relationships of organs, and so on. It is shown that "an entity having the hierarchical type of organization such as we find in the organism requires investigation at all levels and investigation of one level cannot replace the necessity for investigation higher up in the hierarchy" (p. 309). A similar view is expressed by Needham (1936) who states of Wilhelm Roux that "the course he set. . .involved the analysis of development, not into simple physico-chemical processes directly, but into more complex organic processes. He showed that it was possible, and indeed necessary, to deal first with large packets of factors in the biological organism, before proceeding to the finer analysis of the smaller packets."

The application of these notions to community analyses is not difficult to perceive. One way of analysing an ecosystem is to list all the species and, by studying each individually, to discover their various activities and so build up a picture of the community as a food chain. But this method fails to discover many important phenomena characteristic of communities. It is, in fact, studying one level in the hierarchy while ignoring higher levels. The study of the habits of individuals fails to yield any information on the phenomena produced by population interactions, unless these have been the object of previous study. As an illustration we may take a very simple ecosystem, for example, one in which two species of Protozoa, A and B, of which A preys upon B, exist

together with a bacterium, C, which forms the food of B, the physical environment remaining constant. Now if we proceed to investigate the habits of these three species we shall arrive at the food chain $C \rightarrow B \rightarrow A$. Further than this it will not be possible to get.

A much more useful method will be to study first the behaviour of the populations of these species. It will not be necessary to have any previous knowledge of their habits. We may then disover that the populations fluctuate rhythmically and that these fluctuations bear definite quantitative relationships to one another and to the densities of population. We may then proceed to apply the methods used in the first study, and the food chain now discovered explains the fluctuations and a far more complete idea of the working of the community is obtained than could possibly have been arrived at by only studying the habits of the individuals comprising it.

The analysis of the ecosystem in terms of behaviour of individuals, that is, the construction of a food chain, and the correlation of physiological requirements with the physical environment, take no account of a factor of the first importance in descriptions of community behaviour, namely, time. Omission of the time factor in community studies results in a failure to disclose the dynamic nature of the equilibria characteristic of ecosystems and data so obtained are of very limited value.

It is in the belief that in analysis of ecosystems descriptions of population behaviour must precede the study of the physiological requirements of individual species that the present investigation has been made. It is an attempt to describe a small section of a much larger ecosystem, during a small part of its existence, in terms of population change. Previous analyses have shown (Ford, 1937) a similarity of behaviour in ecosystems in which the predominating animals are Acarina and Collembola. This is to be expected since related organisms, having similar physiological requirements, will tend to produce similarities in the phenomena exhibited by the communities they form. Collembola-Acarina ecosystems occur, in temperate regions generally, wherever there is abundance of decaying vegetation and moisture. The period of greatest activity is, in Europe, in winter, during cold wet weather.

The present study endeavours to describe quantitatively the behaviour of a Collembola-Acarina-*Bromus* ecosystem during its period of greatest activity. It has attempted to show approximately the densities of population of its component species at the commencement of winter activity, the time taken in reaching a maximum density and the course of the declining population. In addition to this description of the changes within the ecosystem during the passage of time, the census has permitted a preliminary analysis to be made of the spatial distribution of the various species and the changes in distribution taking place during climatic variation and during alterations in population density. It is not claimed for the data given that they represent more than a rough approximation to reality, but it is believed that the results are suffi-

ciently consistent to allow the major features of this ecosystem, during the time it has been under observation, to be outlined. It is not, of course, to be supposed that the details of the census will be repeated in another season, indeed, this is evident from a comparison of some features of the Brometum populations in the three seasons with which we have been concerned.

11. Summary

1. This paper concludes three series of censuses of a Collembola-Acarina (springtail-mite) community inhabiting tussocks of the grass *Bromus erectus*.

2. Changes in the composition of the fauna of the Brometum during the winters of 1935–6, 1936–7, 1937–8 are reviewed. The principal change was the decline between the first and second winters of the springtail, *Pseudachorutes subcrassus*. This may have been the cause of an increase, subsequently, in the population density of the remaining species.

3. Sampling at different levels revealed a distinct vertical zonation in the grass fauna which is subject to alterations during changes in the moisture content of the habitat. The soil fauna is distinct from that of the grass.

4. A marked positive correlation between the density of the mite *H. pallidulus* with the water content of samples indicates that this species descends to the bases of the grass leaves during relatively dry periods. There is no correlation in the case of *P. subcrassus* nor with Trombidiform mites. *A. aphidioides* has a doubtful negative correlation. This latter species though abundant in 1936–7 showed a declining population with a periodic fluctuation at intervals of approximately 3 weeks throughout that winter. This periodicity was apparently independent of moisture variation, as of other measured climatic factors.

5. Population increase commenced in October, reaching a peak in the middle of December, in each winter. In 1936–7 the decline from this peak was continuous, thus differing from 1935–6 when another increase took place at the end of January. It would appear that the decline following the December peak is independent of changes in the physical environment, though further work on different lines would be needed to investigate a biotic cause, if any.

6. The approximate age distribution of *P. subcrassus* was analysed and shown to correspond, in its changes during the fluctuation, to that expected in a growing and declining population.

7. The distribution of the fauna, expressed in terms of the standard deviation, showed that at the commencement of the population increase variability is high. Variability decreases as the increase in population continues, but increases again with the ultimate decline of the population.

8. A discussion is devoted to the purpose and status of ecosystem analyses.

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POPULATIONS, TERRITORIES AND BIOMASSES OF ANTS AT THORNHILL, YORKSHIRE, IN 1937

By WALTER PICKLES

(*With* 1 *Figure in the Text*)

1. Introduction: changes in nest populations

In the summer of 1937 the survey of ants' nests at Thornhill was repeated. No new species of ants were found, and many of the old nest mounds had become re-inhabited, i.e. nos. 1, 2, 3, 6, 8A, 20 and 21. Of these nests, nos. 1 and 3 were *Acanthomyops* (*Chthonolasius*) *flavus* F.; nos. 6, 8A and 21 were *Myrmica ruginodis* Nyl.; and nos. 2 and 20 were *Formica fusca* L. Nest 21 was a mixed nest of *A. flavus* and *M. ruginodis*. In 1936 only *M. ruginodis* was present, so that the former species must have migrated to the spot. Nest 6, although inhabited again, did not contain the same species as in 1936. Previously *F. fusca* inhabited this nest, but in 1937 *M. ruginodis* occupied it; and even then only as a temporary nest.

In 1936 I marked 50 inhabitants of nests 1, 8A and 15 (a nest of each species) but have been unable to find any of these marked ants, this may possibly have been due to the fact that the mutilated ants were killed or died naturally, or that the whole colony has moved out of my area of census. Nest 15 was not inhabited at all this year (1937); but nests 1 and 8A have been inhabited by the same species again though the populations have decreased in both cases: from 1543 to 152 in the case of nest 1 and from 343 to 187 in the case of nest 8A. If these are members of the 1936 nests, which is by no means certain, then it is quite possible for all the mutilated ants to have succumbed in some way mentioned above.

In the cases of *Myrmica ruginodis* and *Formica fusca* it seems quite likely, from the way stones are inhabited at one time and not at another, that they are generally on the move, staying a few weeks under one stone, and moving on to another, particularly if disturbed.

With regard to *Acanthomyops flavus*, although they are not so active in foraging over the surface of the ground as the other two species, they move from place to place: hence the appearance of this species under the stone of nest 21 in 1937.

2. Discussion of the species

(*a*) *Acanthomyops flavus*

In previous years this species was not noticed to be abroad foraging and it was stated that I had never seen them leave the nest mound (**4**, **5**). Early in the summer months several small colonies of these ants, of say two dozen to thirty or so in number were discovered. I thought, at first, that possibly

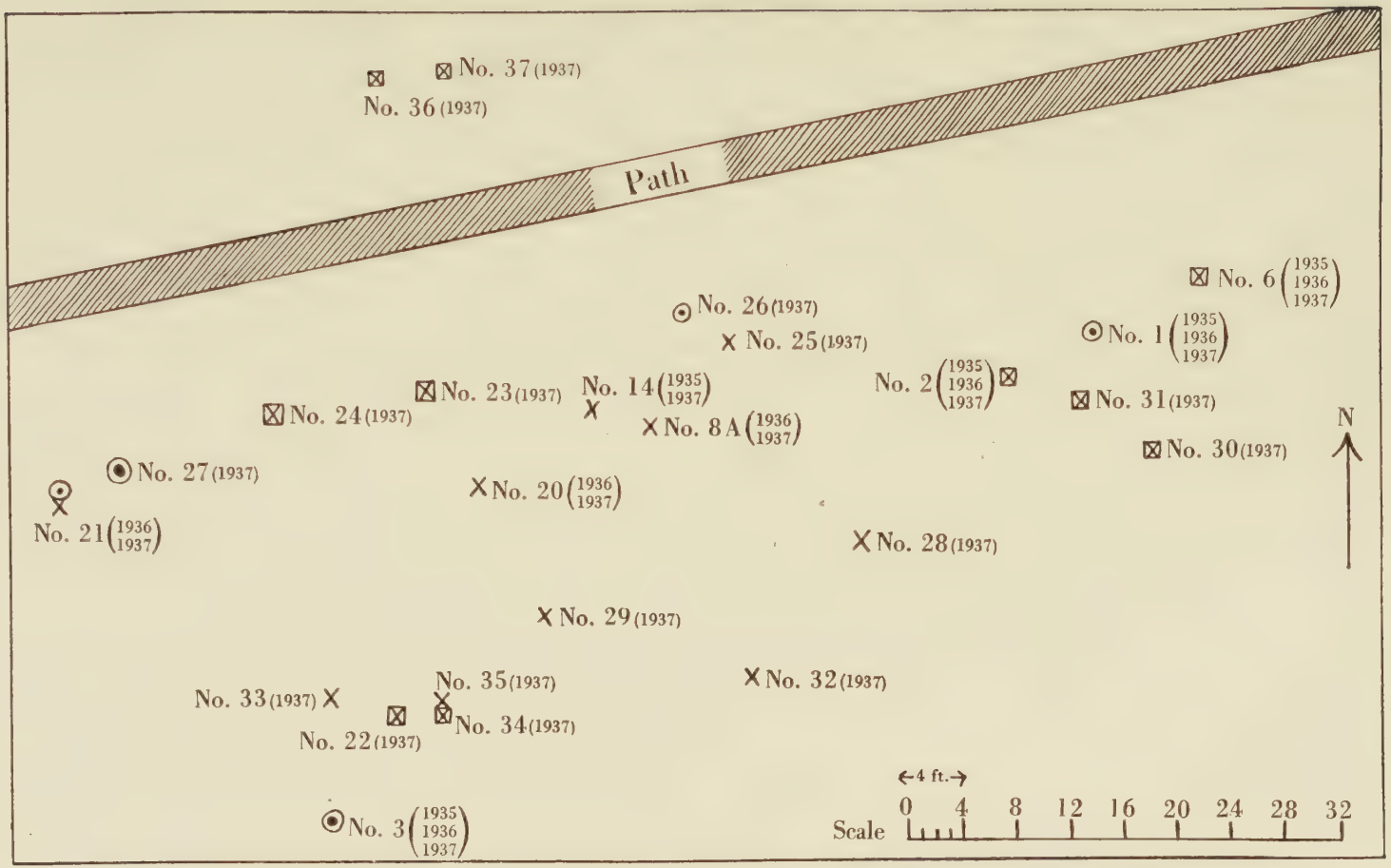

Fig. 1. Plan of nests on the area under observation during 1937. The dates of the nests are in brackets. × nests of *Myrmica ruginodis*; ⊠ nests of *Formica fusca*; ⊙ nests of *Acanthomyops flavus*; ⚲ mixed nest of *M. ruginodis* and *A. flavus*.

having disturbed nests 1 and 3 in the past two summers, the effect had been to distribute many of the inhabitants over the area. However, I found that Carey & Diver (**1**) had found a similar state of affairs at South Haven Peninsula, Dorset. This distribution then was not entirely artificial and I began to dig round the nests to discover whether there was any way of accounting for this distribution. At a spot 8 ft. from nest no. 27 was found a small colony of about a dozen *Acanthomyops flavus* together with about an equal number of *Myrmica ruginodis*. They were on the roots of grass and were attending to some aphides (*Tetraneura ulmifoliae* Baker). I have since discovered specimens of these aphides on the roots of grass in different parts of the area. These aphides may possibly help in the distribution of the species as Theobald (**2**) mentions that the apterous viviparous females are found in ants' nests, e.g. *Lasius* (*Acanthomyops*) *flavus* and *Myrmica ruginodis*.

The aphides, *Tetraneura ulmifoliae*, were found on the roots of the grass, *Holcus mollis*, which grows fairly generally among the bracken and also on nest 27. On other parts of the hillside there are nest mounds completely covered with this grass. Nests 1, 3, 21 and 27 also, are covered with the grass *Deschampsia flexuosa*. The greater number of these nests on the whole hillside are also grass-grown. Possibly there may be some connexion between the long underground roots of *Holcus mollis* with their accompanying aphides and the underground feeding territory of *Acanthomyops flavus*.

With regard to the population figures of this species (see Table 2), the decrease in population of nests 1 and 3 may be largely artificial, due to them having been disturbed in two previous summers. The upheaval has probably caused them either to die off or move to another part of the area. This may be one reason for the great decrease in numbers of no. 1 compared with 1936, as near the stone under which they have lived in 1937 on the mound, there was a heap of dismembered ants. Among this heap were the abdomens, thoraxes and heads of a number of females, which clearly shows that, after the nest had been returned last summer, there was a considerable mortality among the inmates of this nest.

I have mentioned earlier that the ants are constantly moving about from stone to stone. There was one very interesting example of this in connexion with nest no. 27. A flat stone was here used as a nursery. At one period in May and June there were many cocoons beneath this stone. Later in the summer, on 25 August and until 18 September it was out of use. From the latter date until 2 October it has been used as a nursery by *Formica fusca*, *Acanthomyops flavus* still occupying the surrounding ground.

There were altogether 5 nests of *A. flavus*, of which nos. 1, 3, 21 (mixed *Myrmica ruginodis-Acanthomyops flavus*) and 27 were permanent ones and no. 26 was a temporary nest, lasting from 20 May 1937 to 11 August 1937. As a result of digging up the ground round about this nest, several aphides (*Tetraneura ulmifoliae*) were found on the roots of the grass.

(*b*) *Formica fusca*

Of this species of ant, altogether 10 nests occurred, 6 being temporary and 4 lasting throughout the whole summer. The stones of nests 2 and 6 have been occupied during the past three summers; but it is fairly certain that the occupation has not been continuous and by the same ant colonies. Nest no. 2 became deserted altogether and no. 6, which was originally a nest of *F. fusca* (lasting until 6 August 1937), became inhabited by *M. ruginodis* as from that date until previous to 11 August.

There have been cases of temporary sharing of the stone of one species by another. For instance on 4 August 1937 I found the stone of nest 8 A (*M. ruginodis*) being used as a nursery by *F. fusca* (workers and cocoons being under the stone). Two days later when the nest was dug up for counting, they had vanished.

(*c*) *Myrmica ruginodis*

There have been altogether 10 nests of this species of ant, 4 being temporary and 6 being permanent ones. Owing to the very short existence of nest 6 as a *M. ruginodis* nest, from 6 August until sometime previous to 11 August when I paid my next visit, and found it had vanished, it can hardly be called a temporary nest; but rather it seems to have been a "rest" by a nest of ants on the move to new quarters. As mentioned earlier, nest 21 has been a mixed one of *M. ruginodis-A. flavus*.

From this discussion of the species we see that in the case of *A. flavus*, there have been 3 more nests than in 1936, although the 1936 old nests have also been occupied again. In the case of *F. fusca*, there have been fewer permanent nests than there were in 1936, 4 as against 5 in 1936. There have been 10 nests altogether this year, while the total number of nests of this species in 1936 was 7, an increase of 3 nests.

With regard to *M. ruginodis* there have been 10 nests as against 7 last year.

The total number of nests this year has been 25 (reckoning the mixed nest no. 21 as two) as against 16 last year (again counting nest no. 2 of 1936 as two). From this we should expect that there would be an increased population this year, but as the number of permanent nests has been the same as last year (1936) the total population has been roughly the same, being 8246 in 1936 and 8572 in 1937, thus showing a slight increase on 1936.

3. METHODS

Population determinations. As in my previous surveys on ant populations (**3**, **4**, **5**) the ants' nests were dug up and the living inhabitants counted as described previously.

Weights. The same method was used as in 1936 (**5**) for the weight determinations of the nests.

4. Territories

During this survey I have not observed any ant to travel more than the maximum distances recorded in previous years, namely 26 ft. for *Formica fusca* and 10·25 ft. for *Myrmica ruginodis*. This gives a territory of 2124 sq. ft. for *F. fusca* and 330·18 sq. ft. for *M. ruginodis*.

With regard to *Acanthomyops flavus*, arising out of my observations this year, some modification of statements made in my previous records on surveys made in 1935 and 1936 (**4**, **5**) is necessary. In these surveys I stated that *A. flavus* had no feeding territory; but owing to the fact that it has been found attending to the aphid *Tetraneura ulmifoliae* at varying distances away from the nests, then it must have some feeding territory.

I have found isolated groups of *A. flavus* attending these aphides at a distance of 8 ft. from nest 27 under a stone. There were also in this case a number (roughly a dozen or so) of *M. ruginodis* under the same small stone, and crawling about the roots of the grass *Holcus mollis* on which the aphides were situated. Several aphides were picked up by the *M. ruginodis* and carried about, and I observed a specimen of *A. flavus* to pick up an aphid and carry it down a hole. On another occasion a solitary specimen of *A. flavus* was found under a small stone at a distance of 3 ft. from nest 1. Digging around disclosed no other ants about.

Under these circumstances I hesitate to give a definite figure for the feeding territory of this species; but that it has a feeding territory seems certain now.

5. Populations of the nests

The censuses were made by digging up the nests and counting the living inhabitants; males, females, workers and immature forms being counted separately. After being counted the ants were returned to the same spot.

Table 1. *Analysis of populations of nests*

Name of species	Date	No. of nest	Workers ☿	Males ♂	Females ♀	Larvae	Naked pupae	Cocoons ☿	Female cocoons	Total
Acanthomyops flavus	10 July 1937	3	1333	2	1	16	—	124	5	1481
	11 Aug. 1937	21*	1763	25	3	—	—	78	—	1869
	25 Aug. 1937	1	152	—	—	—	—	—	—	152
	8 Sept. 1937	27	1127	—	1	—	—	—	—	1128
Formica fusca	4 Aug. 1937	30	326	—	1	43	127	112	—	609
	27 Aug. 1937	31	333	—	1	—	—	8	—	342
	25 Sept. 1937	36	603	—	4	—	—	31	—	638
	2 Oct. 1937	37	189	—	—	—	—	—	—	189
Myrmica ruginodis	19 July 1937	29	93	—	—	14	5	—	—	112
	6 Aug. 1937	8A	185	—	2	—	—	—	—	187
	11 Aug. 1937	21*	28	24	—	—	—	—	—	52
	11 Sept. 1937	32	456	—	1	—	—	—	—	457
	18 Sept. 1937	33	878	—	1	20	—	—	—	899
	25 Sept. 1937	35	457	—	—	—	—	—	—	457

* Mixed nest of *Myrmica ruginodis-Acanthomyops flavus*.

An analysis of the populations of each nest is shown in Table 1. From this it will be seen that as in previous years the nests of *Acanthomyops flavus* (except nest 1) are the most populous, whilst, on the average, the nests of *Formica fusca* are more populous than those of *Myrmica ruginodis*.

Table 2

Name of species	No. of nest	Population in 1935	Population in 1936	Population in 1937
Acanthomyops flavus	1	5,743	1,543	152
	3	5,613	2,210	1,481
	*21	—	—	1,869
	27	—	—	1,128
	Total	11,356	3,753	4,630
Formica fusca	6	275	720	—
	12	73	—	—
	9	218	—	—
	11	65	—	—
	13	143	352	—
	17	—	766	—
	19	—	13	—
	†2	249	482	—
	15	—	56	—
	30	—	—	609
	31	—	—	342
	36	—	—	638
	37	—	—	189
	Total	1,023	2,389	1,778
Myrmica ruginodis	†2	279	78	—
	10	1,534	—	—
	14	233	—	—
	8	660	(8A) 343	(8A) 187
	5	—	1,159	—
	18	—	489	—
	*21	—	35	52
	29	—	—	112
	32	—	—	457
	33	—	—	899
	35	—	—	457
	Total	2,706	2,104	2,164

* Mixed *Myrmica ruginodis-Acanthomyops flavus* nest.
† Mixed *Formica fusca-Myrmica ruginodis* nest.

In Table 2 a comparison of the populations of the nests in the three years 1935–7 is shown. From this table we see that the population of *Acanthomyops flavus* has increased by 877 on the 1936 census. *Formica fusca* shows a decreased population of 611 on 1936, though, on the average, the nests have been more populous. In the case of *Myrmica ruginodis* the population has remained approximately the same with a slight increase of about 60, though the average population per nest has decreased from 420 to 360. In the three years during which censuses have been taken, the *Myrmica ruginodis* population has fluctuated least of all three species.

Again I found that the stone covering a nest or the mound of one only gives an approximate idea of the size of the population in it (Elton (**6**), Pickles (**3**, **4**, **5**)).

6. Density of population

The density of population may be expressed in three ways: (*a*) the *Economic Density*, i.e. the total population divided by the territory; (*b*) the *Lowest Density*, i.e. the total population divided by the area of the census; and (*c*) the *Greatest Density*. The greatest density is taken as the population of the nests at night. As the nests were dug up either in the early morning or evening, the total populations given may be counted as the greatest densities.

Owing to the fact that at least a definite illustration of the existence of territory among *Acanthomyops flavus* has been given, a provisional "territory per nest" and economic density will be given in Table 3. A definite figure, however, can be given for the lowest density. For density purposes nests 36 and 37 were practically on the verge of the area, and therefore only half of the territory of each nest actually came within the survey. The total territory of these two nests will, therefore, count as one for that species.

Table 3. *Densities of population*, 1937

Name of species	Total population*	Territory per nest	Economic density = Total population / Total territory	Lowest density = Total population / Area of census†
Acanthomyops flavus	4423	3·14 sq. yd.	352·149 per sq. yd.	4·204 per sq. yd.
Formica fusca	1500	236·00 sq. yd.	2·118 per sq. yd.	1·425 per sq. yd.
Myrmica ruginodis	2159	36·70 sq. yd.	9·804 per sq. yd.	2·052 per sq. yd.

* Pupae are not included in this number.

† The area of the census is 1052 sq. yd.

From Table 3 it is seen that *Acanthomyops flavus* has the highest economic density and *Formica fusca* has the least.

The species having the greatest lowest density is *A. flavus*, with *M. ruginodis* second, and *Formica fusca* least. The lowest densities of both *F. fusca* and *M. ruginodis* are approximately the same as they were in 1936, namely 1·425 (1937) and 1·471 (1936) for *F. fusca* and 2·052 (1937) and 1·859 (1936) for *M. ruginodis*.

7. Weights of the populations

After each nest had been counted, the inhabitants were weighed and an analysis of these weights is given in Table 4. According to Gause (**7**) the biological success or failure of a species can be shown by the weights of the living creatures.

In the case of the three species under observation, the total weights of all the living ants were:

Acanthomyops flavus = 2·859 g. (7·037 g. in 1936)
Formica fusca = 5·388 g. (9·616 g. ,, ,,)
Myrmica ruginodis = 4·438 g. (3·665 g. ,, ,,)

These figures show that, as in 1936, *F. fusca* has the greatest weight, though this, like the population, has fallen from its value of the previous season.

Table 4. *Analysis of the weights of the nests (in g.)*

Name of species	No. of nest	Workers ☿	Males ♂	Females ♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	Total
Acanthomyops flavus	3	0·926	0·001	0·010	0·009	—	0·187	0·057	1·190
	21*	1·040	0·012	0·034	—	—	0·030	—	1·116
	1	0·087	—	—	—	—	—	—	0·087
	27	0·453	—	0·013	—	—	—	—	0·466
Formica fusca	30	0·851	—	0·024	0·094	0·321	0·311	—	1·601
	31	0·997	—	0·010	—	—	0·017	—	1·024
	36	2·163	—	0·095	—	—	0·163	—	2·421
	37	0·342	—	—	—	—	—	—	0·342
Myrmica ruginodis	29	0·195	—	—	0·290	0·110	—	—	0·595
	8A	0·299	—	0·004	—	—	—	—	0·303
	21*	0·041	0·026	—	—	—	—	—	0·067
	32	0·812	—	0·002	—	—	—	—	0·814
	33	1·768	—	0·003	0·004	—	—	—	1·775
	35	0·884	—	—	—	—	—	—	0·884

In the case of *A. flavus*, although the population has increased by nearly 900 on that of 1936 the weight has decreased greatly. This is due to the fact that fewer females and female cocoons have been found in the nests dug up for counting.

M. ruginodis shows an increased weight over the previous season, although the population has remained roughly the same. This is, no doubt, due to fewer larvae being found and more adults being present, 4 out of the 6 nests having no immature forms.

8. The biomasses of the species

The success or failure of the species can be also expressed as the biomass, i.e. the total weight of material per unit area.

Table 5. *Biomasses*

Name of species	Total wt. in g.	Area of census in sq. m.	Wt. per sq. m. in g.
Acanthomyops flavus	2·859	880·51	0·003
Formica fusca	5·388	880·51	0·006
Myrmica ruginodis	4·438	880·51	0·005

F. fusca has the greatest biomass and *A. flavus* the least. The biomass of *M. ruginodis* has increased from what it was in 1936 (i.e. 0·004) and *F. fusca* has decreased from 0·011 to 0·006 g. per sq. m. From this fact and also that the number of nests of *M. ruginodis* has increased, it seems very likely that this species is on the increase in this particular area.

9. Relations with other nests

Often when the stones were lifted up to observe the nests, specimens of the Thysanuran, *Campodia staphylinus*, were crawling about on the under side of the stone and among the ants. This has occurred with all three species of ants. The ants appeared to take no notice of them –they crawled about and eventually disappeared down holes in the soil. Donisthorpe (**8**) says there are no

myrmecophilus species of Thysanura in Britain. I therefore conclude that the *Campodia* were there purely by accident, as when they were more numerous under a stone covering a nest, they were also plentiful under stones on the rest of the area which were not occupied by ants. The fact that they crawled about amongst the ants when the stone was lifted may be due to the movement throwing them down. In any case I did not observe any of these insects to be attacked by ants; but rather the latter seemed totally indifferent to their presence.

In the layer of decayed bracken leaves and amongst the lower parts of the tufts of grass there were numerous specimens of the Collembolan, *Entomobrya multifasciata.*

10. Conclusions

From this survey, several points of interest have arisen. First, owing to the fact that on several occasions both *Myrmica ruginodis* and *Acanthomyops flavus* have been found attending the same species of aphid (*Tetraneura ulmifoliae*) there may be to some degree a struggle for existence between these two species in the area. If one species of ant is acted upon it should, therefore, produce an effect on the other. This has occurred to some degree.

By the repeated digging up of the nests of *A. flavus*, the population has substantially decreased from what it was in 1935 when it then represented things as they were before any disturbances of an unnatural character had occurred. Although the *Myrmica ruginodis* population has remained approximately the same as in 1936, the fact that the number of nests has increased shows to some degree that this species is inclined to be in the ascendant. The reduction of the population of *A. flavus* may have played a part in this change.

Secondly, the repeated digging up of nests for observation hardly seems a success with *Acanthomyops flavus*. The great reduction in population of this species is not quite a natural event, I am afraid, but is due to the ants being disturbed. The two nests, which have existed through the three seasons, have decreased in population in the case of nest no. 1 from 5743 (1935), 1543 (1936) to 152 in 1937 and in the case of nest no. 3 from 5613 (1935), 2210 (1936) to 1481 in 1937. I found that in the case of nest 1 there had been considerable mortality since 1936. Possibly the ants of the two new nests, 21 and 27, have come into the area from the surrounding region.

With regard to the other two species of ants I feel that the method used in these surveys is quite suitable, partly owing to the movements of the ants from stone to stone, and there does not seem to be any mortality when returned to their nests. Artificial disturbances have not the same disastrous effects on them as on *Acanthomyops flavus*.

11. ACKNOWLEDGEMENTS

I wish to thank Mr H. St J. K. Donisthorpe for naming the ants; the Agent to the Savile Estate, Mr C. A. E. Horton, for renewing permission to use the land; Mr H. Wright, Principal of the Technical College, Dewsbury, for allowing me the use of the Balance Room in the Chemical Department; experts at the Natural History Museum, London, Mr Frederick Laing, aphides and Mr F. G. Westropp, Thysanura and Collembola; Dr T. W. Woodhead, grasses; and Mr Charles Elton for encouragement and suggestions.

12. SUMMARY

1. A survey of three species of ants living on a portion of a hillside at Thornhill, Yorkshire, was repeated in 1937, the object being to record the fluctuations of populations and biomasses.

2. *Territory.* No increase of territory of the two species *Formica fusca* and *Myrmica ruginodis* was observed. It was, however, found that *Acanthomyops flavus* does forage for food and attends the apterous viviparous females of the aphid *Tetraneura ulmifoliae*, which are on the roots of the grass *Holcus mollis*.

3. *Populations. Acanthomyops flavus* showed an increase of population due, no doubt, to immigration from surrounding regions. *Formica fusca* showed a decreased population from that of 1936, while that of *Myrmica ruginodis* was roughly the same.

4. *Densities of population. Acanthomyops flavus* showed the greatest economic density and *Formica fusca* the least. The lowest densities of the three species were in the same order.

5. *Weights and biomass.* After the census of each permanent nest had been made, the occupants were weighed and the biomass was found. From these calculations *Formica fusca* was found to have the greatest weight per sq. m. This was followed by *Myrmica ruginodis*. However, *Myrmica ruginodis* seems to be in the ascendant, as both in number of nests, in biomass and in actual weight it has shown increases on the 1936 figures.

6. The Thysanuran, *Campodia staphylinus*, was found abundantly under the stones and under stones covering the ants' nests, especially after rain, and the Collembolan, *Entomobrya multifasciata*, was found amongst the decaying layer of bracken, grass, etc., covering the area.

7. The method of repeated digging up of nests for censuses hardly seems suitable for determining the populations of nests of *Acanthomyops flavus*. The other two species seem to suffer less disturbance and mortality by it.

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CANADIAN ARCTIC WILD LIFE ENQUIRY, 1936–37[1]

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(*With 4 Figures in the Text*)

1. Introduction

This is the second report based on questionnaire enquiries into the annual changes of abundance of certain species of animals living in the Canadian Arctic and Labrador. The previous report should be consulted for a discussion of the species under investigation, the form of questionnaire used, and a full description of the methods of mapping replies. Fluctuations in abundance of the arctic fox (*Alopex lagopus*) are one of the vital factors in the economy of the Canadian North, affecting at the same time both the fur trade and native welfare. They are the practical aspect of a remarkable periodic oscillation in animal populations which in any case deserves study on account of its scientific interest. This oscillation affects also lemmings (*Lemmus* and *Dicrostonyx*) which form one of the chief food supplies of the arctic fox. It is the purpose of this enquiry to make as full a record as possible of the fluctuations, and if possible to correlate those of the fox with changes in its food supply, particularly lemmings, and also with climatic and other variables. The snowy owl (*Nyctea nyctea*) is also closely dependent upon lemmings, and its fluctuations may prove to be a useful index of the abundance of this basic food-animal, and therefore of fluctuations in the fur crop.

Outbreaks of epidemic disease among sledge dogs are another important factor in the life of the North. The possibility of correlation between these epidemics and mortality periodically affecting wild life is a fourth aspect being followed in this enquiry.

Questionnaires are sent out by the Northwest Territories Administration, Ottawa. Full co-operation has been given to the Bureau of Animal Population by the authorities, in particular by the Commissioner of the Northwest Territories, Dr Charles Camsell, and the Deputy Commissioner, Mr R. A. Gibson. The Governor and Committee of the Hudson's Bay Company have kindly allowed full use to be made of their annual zoological reports, and the Company's Fur Trade Commissioner in Winnipeg, Mr Ralph Parsons, and his staff, have given extensive co-operation. Mr Charles Elton has given me considerable help, and we wish to thank the many observers on the results of whose judgment this report is based.

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

Forty-six replies were received through the Government enquiry and sixty-five from Hudson's Bay Company posts in the Arctic. Information from the more southerly posts of the company has also been included in the case of the sledge dog. The enquiry is being continued.

2. Methods

The enquiry relies for its measure of changes in abundance upon opinions given by field observers, which are mapped by methods that have been made as objective and free from bias as possible. There is no doubt that these carefully standardized methods of mapping introduce very little distortion of the opinions expressed in the questionnaire replies. From the scientific point of view it is of greater importance to consider how far the observations made in the field are themselves liable to the errors that must necessarily enter into any subjective method of estimating changes in wild animal populations. Factors tending to reduce these errors are the great amplitude of the fluctuations observed, the year-to-year method of comparing abundance, and the fact that the observations are not only based upon individual experiences but in many cases also on those of other people, including native hunters familiar with wild life in the field. It is believed that the system of recording and mapping adopted is sufficiently reliable to give a substantially correct general picture of the wild life situation from year to year. It is in any case the only type of method at present applicable to the measurement of current biological phenomena over so huge an extent of country as the Canadian Arctic.

In Table 1 are listed the opinions of observers about abundance for the 12 months ending 31 May 1937, compared with the previous 12 months. The number of observers reporting "increase", "decrease" or "no change" is counted in each of the regions and summarized in Table 2 to give the main statistics for this report. The maps (Figs. 1, 3, 4) show the areas to which these reports apply. From the number of arrows indicating each kind of reply further statistics (Table 3) are obtained. These figures represent roughly the percentage area reporting "increase", "decrease" or "no change", each arrow representing an area of 2500 sq. miles. (For example, an area of 50 miles radius = 7900 sq. miles gets 3 arrows = 7500 sq. miles.)

When there are a number of adjacent areas from which similar reports are received it is possible to space the arrows so that their number gives a fair approximation to the total area involved. However, when no such unanimity is reached a regular pattern cannot be made and the approximation to the true area is less accurate. In this case the total number of arrows is counted and from it is subtracted a certain number of the arrows in disagreement, as shown in Table 3 by the small index figures. This may give a slight underestimate of the size of the area because an arrow is taken as contradicting another of different sign when there is any overlapping of the areas represented by the

two arrows. For this purpose these areas are considered to be strips "25 by 50 miles" along each side of the long axis.

The lemming reports in Group 9 may be taken as an example of the method of working out the percentage area covered by each type of observation. Here nine arrows are in disagreement: three of "decrease" contradicted by *three* of "no change", one of "decrease" contradicted by *one* of "no change" and *one* of "increase". The approximate area involved is therefore roughly 2500 sq. miles times the total number of arrows (eighteen) less *five*. Of this number, eight indicate "no change", but four are contradicted. The percentage by area reporting "no change" may therefore be expressed as between $\frac{4 \times 100}{13}$ and $\frac{8 \times 100}{13}$, or 31–62%.

The advantage of such a method is that it gives a measure of the reliability of the observations. However, care must be taken to limit the weight given a single observer; and an arbitrary upper limit of ten arrows per person has been adopted. This limitation is achieved by spacing the arrows out from the centre of an area of large diameter. However in the case of one observer (No. 32 in Group 7) the area covered was not a solid block of country but several long stretches, mainly coastal. Here ten arrows have been spaced out over the area on the assumption that each represents an elongated area of 2500 sq. miles instead of a square. This procedure was less complicated than others to apply and also gives a probably less exaggerated representation of the area than would a closer spacing with more arrows. No such large areas were described in the previous report. Thus, while the maps are principally designed to convey a comprehensible diagrammatic picture, they have been constructed with the further aim of obtaining statistics on a basis of area covered.

Reports on "mice" are given by many observers, and where abundance or increase is stated this is listed but not mapped or analysed. Some of the lemming reports may perhaps refer to mice but this error is not considered serious. In any case both are an important source of food for predatory species.

It should be mentioned that the data have been treated as objectively as possible and no attempt has been made to cover up even obvious misstatements. This course is considered preferable to anything that would lay the results open to the criticism of being engineered. In two instances, however, some discretion has been observed in mapping the present data. In Group 1 (Northern Labrador) mapping has been confined to the coast as it is considered that the two larger areas described in the Hudson's Bay Company reports were meant to apply less to the arctic animals than to the other species also covered by the reports. In Group 2 it has been decided to omit the Fort McKenzie report from the calculations (though it has been mapped) since the other reports in this group all refer to phenomena on the coast or inland a distance mostly less than 70 miles. Thus the ten arrows allotted this post would have unduly

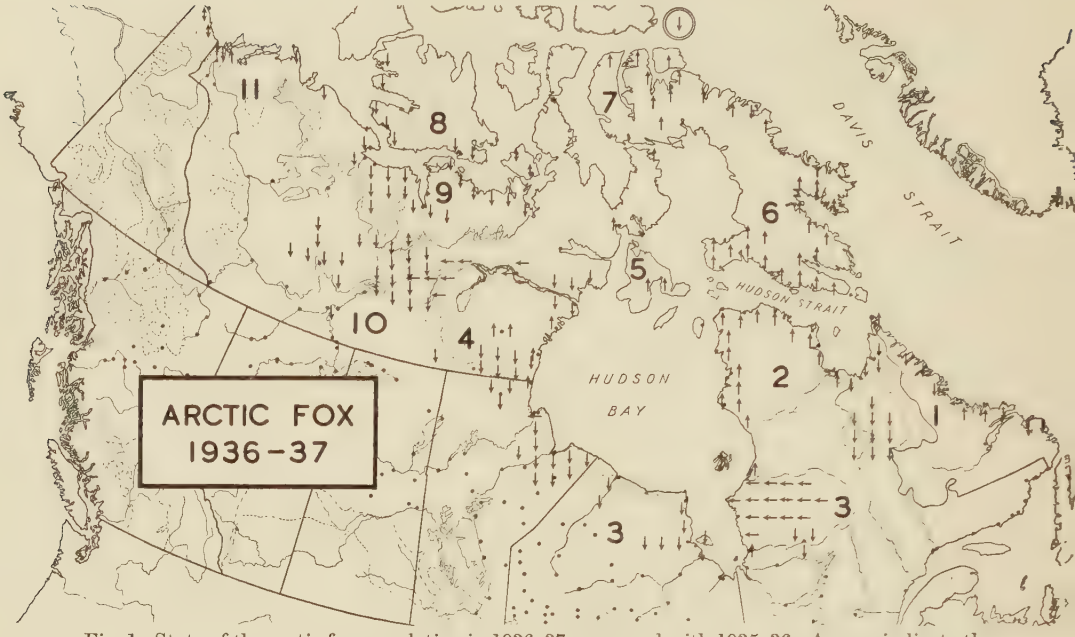

Fig. 1. State of the arctic fox population in 1936–37 compared with 1935–36. Arrows indicate the areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

Fig. 2. Prevalence of disease among sledge dogs in 1936–37. Reports of disease are indicated +; disease absent or in minor proportions ○. Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.

Fig. 3.

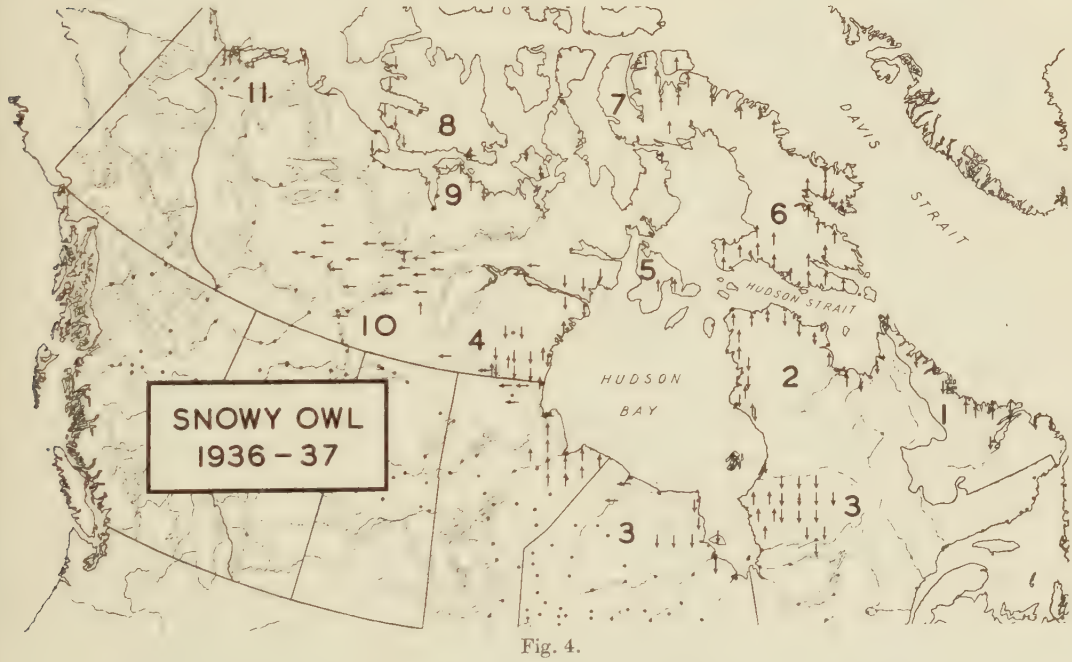

Fig. 4.

Figs. 3, 4. State of the lemming and snowy owl populations in 1936–37 compared with 1935–36. Arrows indicate areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

influenced the results in this group. In any case lemmings were stated in a report for 1932–33 to be very scarce at all times round this post. In Group 3, south of the breeding range of the arctic fox, all the areas have been mapped in full.

In the maps of sledge dog reports (Fig. 2) a circle indicates that a definite report has been received of absence of serious disease, a plus sign that an outbreak has occurred as described in Table 4 (*a*). One sign only is given per observer except when two or more distinct localities are described. The Hudson's Bay Company observers are only asked to give details when disease is present: thus lack of a specific statement may be taken to imply that disease was absent, though actually no circle is put on the map.

3. Results

Lemming. The most striking feature of the 1936–37 results is the unanimity of reports of increase over the whole huge extent of Baffin Island. During 1935–36 there were only two such reports, in the south-eastern part of the island, so that a remarkable regional recovery is indicated. This upward trend of the lemming population was also shown, to a lesser extent, along the northern fringe of the Quebec Peninsula from Hebron in Labrador to Port Harrison in Hudson Bay. Although reports of continued scarcity or decrease came from several places, the contrast with 1935–36 is well marked. Increase among "mice" or lemmings or both was reported fairly commonly from James Bay and the south and west parts of Hudson Bay in 1935–36, and this increase was apparently well maintained in 1936–37: on the north-west side, as far as Tavane. North of this there was continued scarcity and decrease, and in Group 5 the increase previously reported was reversed.

In the Western Arctic no broad regional trends are apparent and the prevalent scarcity from 1935–37 undoubtedly made comparisons extremely difficult. It should be noted, however, that in the vicinity of King William Island and Cambridge Bay and the mainland south of these points, lemmings were reported well on the increase. This is confirmed by some later information reaching Cambridge Bay by dog team on 19 June from the post manager at King William Island: "Lemming and mice in immense numbers crossing from mainland to islands northward. Thousands were drowned on the ice crossing over" (Postscript to report No. 30).

Elsewhere in the West there was scarcity of lemmings, correlated with scarcity of arctic foxes and snowy owls. A notable exception was Baillie Island: "It was only in late April and early May that there was any great number of both white foxes and coloured foxes in this locality. The white foxes were coming in off the ice in May steadily, more than in any other spring that we remember. Perhaps they were following the lemming, whose tracks (and often the animals themselves) could be seen even for miles out on the ice. The

land was overrun with them. The snowy owl can be seen everywhere, sitting on the tops of knolls, and the natives report that many of the nests have as many as fifty dead mice scattered around them."

A further report (No. 31) may be quoted as showing some of the difficulties of making exact reports for large areas:

Thelon Game Sanctuary. In a considerable area in which lemming were scarce last year they were more abundant (western portion). In certain parts of this region where they were abundant in 1935 they are now less so. In the eastern region (towards Baker Lake) many patches of abundance were left though there were signs of a heavy decline in many places not long previous to this summer. I was told that many bodies were to be seen at break-up at Baker Lake. After break-up I noted windrows of lemming dung on the shores of Aberdeen and Shultz Lakes—which are hard to explain unless the animals were on the lake ice and on the Thelon river ice in numbers.

Arctic fox. In 1935–36 no less than 91% of all observers reported decrease, and only 4% increase. In 1936–37 a considerable difference appeared between Eastern and Western Arctic reports and it has been necessary to consider them separately. In the East, 57% of observers reported increase, and this was particularly noticeable in Baffin Island and along the coast of Northern Quebec. The increase was stated at Diana Bay to have been "about 6 : 1, a rather surprising increase over last year".

There is only small evidence of increase elsewhere in Hudson or James Bay, especially outside the breeding range of the arctic fox, south of the tree limit. However, it must be pointed out that there was only one report of increase (in Group 1) from the whole of the Eastern Arctic in 1935–36 so that a definite improvement is indicated. In the Western Arctic only 11% of observers claimed that increase had taken place, and these reports were almost entirely contradicted, for by area the increase was only 2–13%. Report No. 41 (Group 11) states: "It is thought by local trappers that white foxes are now definitely on the increase in this area. The increase is slow but steady, although a sudden increase might occur at any time, not from breeding in the district but by the arrival of a migration, probably from arctic islands, under suitable conditions of ice."

Snowy owl. There is again remarkable unanimity in the reports of increase from Baffin Island, and this, like the increase in foxes, seems to be correlated with an increase of lemmings.

Baffin Island, south coast (No. 27). An Eskimo said he had seen seven snowy owls in one day, in the vicinity of Markham Bay in October 1936. This is an unusually large number to be seen in one day on any part of the south coast of Baffin Island.

A further correlation exists between reports of increase of lemmings and snowy owls along the coast between Hebron and Port Harrison. Out of ten reports of lemming increase no less than eight were accompanied by similar reports of increase for the snowy owl. Owls were scarce in the southerly Group 3 and had

not increased on the west coast of Hudson Bay as much as the 1935–36 reports might have led one to expect. Increase on Southampton Island was apparently not correlated with increase in lemmings; but from the King William Island–Cambridge Bay vicinity, although some conflicting reports were received, increase seems to have accompanied an increase in lemmings, though it was perhaps of a patchy nature. Farther west, except in the vicinity of Baillie Island, there seems to have been a great scarcity of snowy owls for another year.

Sledge dog. Sledge dogs appear to have been comparatively free from disease in the Arctic during 1936–37. However, there have been outbreaks along the coast of Northern Quebec, though none of a very extensive nature. Three reports from the Western Arctic were couched in rather general terms so that it is not certain that they referred to the period under consideration.

It has been decided to extend the area covered by the enquiry to all of the Hudson's Bay Company posts reporting "dog sickness". The results show that there were several severe outbreaks of distemper in parts of Northern Manitoba and Saskatchewan and in the eastern corner of Quebec Peninsula.

Table 1. *Summary of original data on arctic fox, lemming, snowy owl and sledge dog (part) for* 1936–37

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, r. = rare, s. = scarce, × = not noticeably scarce or abundant, a. = abundant, v. = very.

Sledge dogs: 0 indicates a report that disease was entirely absent. $0^{3,8}$ = report of disease in minor proportions as specified in Table 4 (*b*). + = prevalent disease as specified in Table 4 (*a*). Bracketed observations in the sledge dog column are represented by the same symbol in the map. One symbol is given each observer except where indicated (2).

Square brackets indicate observations that have been partly or entirely omitted from either the map or the calculations—see text.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received directly from the Hudson's Bay Company.

		Arctic fox	Lemming ["Mice"]		Snowy owl	Sledge dog
	Group 1. Northern Labrador coast					
	Frenchman's Island, outside islands and 30 miles inland	D. s.	—		D. s.	+[1]
	Cartwright	D. v.s.	—		D. v.s.	+[2]
	Rigolet: half-way to Cartwright; half-way to Makkovik; one-third way to Northwest River	D. v.s.	D. v.s.		D. v.s.	—
	Northwest River [and inland 400 miles by trappers' reports] ...	r.	D. v.s.		D. v.s.	0^{3}
	Makkovik, 30 miles north and south [and 100 miles inland from head of bays]	I.	—		I.	—
	Hopedale and 30 miles radius ...	I. ×	—		I. s.	—
	Davis Inlet and 30 miles radius ...	N. s.	—		I. s.	—
	Nain and 35 miles radius	D. v.s.	N. s.		D. v.s.	—
	Nutak	D. v.s.	s.	a.	D. v.s.	—
	Hebron and 50 miles radius ...	D. s.	I. a.	I. a.	D. s.	—
	Port Burwell	I.	I. a.	I. v.a.	I.	—
34.	Port Burwell	I. ×	N. ×		v.s.	0

Table 1 (*cont.*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
	Group 2. Coast of Northern Quebec, south to Richmond Gulf and inland					
	Georges River and 50 miles radius	D. s.	I.	I.	—	+[4]
	Whale River to Georges River ...	D. s.	D. s.		D. v.s.	—
	Fort Chimo and 25 miles radius ...	D. v.s.	D. ×		D. ×	+[5]
	[Fort McKenzie and 120 miles radius]	[D. v.s.]	[D. v.s.]	I.	—	—
	Leaf River and coastal area between Payne and Koksoak Rivers ...	I. ×	I. a.	I. a.	I. ×	0
	Payne Bay to Hopes Advance Bay and Aupalook Bay	I. ×	I.		I. ×	—
	Diana Bay, the islands, coast and inland 60 miles	I. ×	I. ×		I. ×	—
	Stupart Bay, west to East Sugluk, south to Diana Bay	I. s.	D. s.		D. s.	0
	Sugluk West and 60 miles radius ...	I. ×	I. a.	I. a.	I. ×	+[6]
	Wolstenholme; 30 miles east and 120 miles south	I. ×	I. a.		I. a.	—
	Cape Smith, inland 50, south 20 and north 70 miles	I. ×	I. ×		I. ×	+[7]
	Povungnetuk and 60 miles radius ...	I. ×	D. s.		D. s.	—
	Port Harrison and 70 miles radius...	I. ×	I. ×		I. ×	—
28.	Port Harrison district, from Kogatuk Bay on the north to Broughton Island	I. ×	D. ×		D. ×	0
	Group 3. South parts of Hudson Bay, James Bay and inland					
	Belcher Islands	I. s.	—		I. s.	—
	Great Whale River north to Richmond Gulf	I. s.	–	I. a.	D. s.	—
	Fort George and 100 miles radius ...	N. v.s.	—		I. v.s.	—
	Kanaapuscow, north, west and south 100 miles; east approx. [800 miles]	N. s.	—	I.	D. v.s.	—
	Eastmain	I. s.	—	I.	—	—
	Neoskweskau and 50 miles radius ...	D. s.	—		D. s.	—
	Albany; 50 miles south, 20 miles north and 40 miles from coast ...	—	—	I.	D.	—
	Attawapiskat; south to the Lawashi River, 150 miles inland, north to Cape Henrietta Maria and Agamiski Island	D. s.	—	I. a.	D. s.	—
	Severn and 100 miles inland ...	D. s.	—		N. ×	—
	York Factory and 120 miles radius	D. s.	—	I. a.	I.	—
	Group 4. West coast of Hudson Bay, north from Nelson River					
	Churchill and 50 miles radius ...	N.	—		N.	—
	Caribou and 50 miles radius ...	D. s.	N. ×		N. ×	—
	Nonala and 20 miles radius... ...	I. ×	I. ×		I. ×	—
5.	Lat. 60°–61° 15′ and from west coast of Hudson Bay to east side of Nueltin Lake	D. v.s.	I.		D. ×	—
	Cape Churchill to Eskimo Point; inland to Windy Lake	—	–		—	0
8.	Lat. 60°–61° and between Nueltin Lake and Sadiah Lake (100 miles west of Hudson Bay coast) ...	s.	I. ×	v.a.	I. s.	0
	Nueltin Lake	D. v.s.	I. v.a.	I. v.a.	N.	—
	Stony Rapids, north-east of, at Snowbird Lake	D. s.	N. s.		N. ×	—
17.	Eskimo Point	I. a.	—		s.	0
	Eskimo Point and 40 miles radius ...	I. ×	I. v.a.	I. v.a.	I.	0
	Padley and 40 miles radius	I. a.	—	I. a.	D. s.	—
	Tavane and 50 miles radius ...	I. ×	I. a.	I. a.	I. ×	—
	Chesterfield to Cape Fullerton; south to Rankin Inlet and 100 miles inland	D. s.	D. s.		D. s.	0
	Baker Lake and 50 miles radius ...	N. ×	D. ×		N. ×	—

Table 1 (*cont.*)

		Arctic fox	Lemming ["Mice"]	Snowy owl	Sledge dog
	Group 5. Southampton Island and Repulse Bay				
	Repulse Bay and radius of 5 miles...	I. ×	D. s.	×	—
	Southampton Island: south Bay ...	I. s.	D. s.	I. a.	—
	Group 6. Southern Baffin Island				
	Lake Harbour east to Pritzler Harbour, west to west side of Markham Bay (native reports)	I. v.s.	I. ⁄	I. ×	–
27.	Eastern end of Frobisher Bay to Nuwata, Foxe Peninsula, on the south coast of Baffin Island	I. v.s.	I. ×	I. ⁄	0
	Cape Dorset; Foxe Peninsula east to Amadjuak Lake; north to south end of Nettilling Lake	I. ⁄	I. ⁄	I. ×	—
	Frobisher Bay, south-east to Waddell Bay, north-east to Sylvia Grinnell River, down west side of Bay to Newell Sound	I.	I. s.	I.	—
33.	Pangnirtung Fjord and other areas adjacent to Cumberland Gulf ...	I.	I. a.	I. a.	0
	Pangnirtung Fjord and Cumberland Sound	I. ×	I. ×	I. ×	
	Group 7. Northern Baffin Island and north				
	Clyde and 35 miles radius	D. ×	I.	I.	—
32.	Pond's Inlet, south to Home Bay, south-west to Igloolik, north-west to Arctic Bay; south shore Bylot Island	I. a.	I. v.a.	I. ×	0
	Pond's Inlet, Eclipse Sound and inland south-west	I. ×	I. ×	I. ⁄	–
	Arctic Bay and north coast of Baffin Island	I. v.s.	I. ⁄	v.s.	—
	Craig Harbour, Ellesmere Island ...	D. v.s.	I. v.s.	v.s.	0
	Group 8. Boothia Peninsula and islands west				
	King William Island and vicinity ...	D.	I.	I. v.a.	—
39.	King William Island*	I. ×	I. ×	D. s.	0
40.	Cambridge Bay vicinity, Victoria Island	D. v.s.	I. a.	N. ×	0
36.	Cambridge Bay and 50 miles radius	D. v.s.	I. v.a.	—	—
	Cambridge Bay only	—	—	I. v.a.	0
	Reid Island and from Lady Franklin Point to north shore of Prince Albert Sound	D. v.s.	D. v.s.	D. v.s.	0
	Fort Collinson, Walker Bay, north to Deans Dundas Bay, south to Minto Inlet	D. s.	D. s.	D. s.	0
	Group 9. Adelaide Peninsula, west to Coppermine River, and inland to Back River				
39.	Mainland around mouth of Perry River*	[I. ⁄]	[I. ⁄]	[D. s.]	0 (2)
30.	Back River to Cambridge Bay ...	D. s.	-	–	—
	Perry River district to Cambridge Bay	-	I. v.a.	I.	0[8]
	Bathurst Inlet and inland for 100 miles east and west	D. s.	D. s.	—	—
38.	Baillie Bay, Arctic Sound	D. v.s.	D. ×	×	0
	Kugaryuak and inland to Red Rock Lake [and Napaktolik]; east to Burnside River	D. s.	N.	—	–

* The same observer is not included in more than one group in Table 2.

Table 1 (*cont.*)

		Arctic fox	Lemming ["Mice"]		Snowy owl	Sledge dog
3.	Back River, Beechey Lake, Musk-ox Lake and Fry Lake districts ...	I. ×	I. ×		×	0
21.	North of west end of Aylmer Lake	D. v.s.	D. ×		D. v.s.	—
	Fort Reliance	—	—		—	0
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
31.	Thelon Game Sanctuary. (For lemming: western portion of Sanctuary, I; eastern portion, D)	N.	* I. D		—	—
9.	Ptarmigan Lake, Clinton Colden Lake	N. s.	D. v.s.		N. ×	—
	Fort Reliance	—	—		—	0
15.	Lynx Lake, headwaters Thelon River, Reliance district	D. v.s.	N.		I. v.a.	0
22.	Whitefish Lake—east to [Granite Falls] on Thelon River	v.s.	I. s.		s.	+[9]
7.	Lat. 62°–65° and Long. 104°–110°, excluding Thelon Game Sanctuary ...	D.	—		r.	
	North-east of Reliance to Thelon Game Sanctuary thence south-east to Whitefish Lake, thence west to Reliance	—	I.			—
	Snowdrift and Reliance	—	—		—	0 (2)
	Snowdrift and between Lat. 62°–65° and Long. 105°–111°	D. v.s.	D.		N.	0
11.	East end of Great Slave Lake ...	D. v.s.	—		v.s.	+[10]
23.	Resolution district and Slave River Preserve	D. v.s.	—		N. s.	0
45.	Yellowknife River, north shore of Great Slave Lake	—	I. v.a.	I.		0
37.	Yellowknife Bay and radius of 40 miles north and east	—	N.		v.s.	0
	Fort Rae, south-east to Yellowknife River, west to Indian village on Grandin River entering Lac La Marte, north-east to Snare Lake district, north to Hottah Lake ...	D. v.s.	—		v.s.	
24.	Fort Rae to Snare Lake, Providence Lake and Lac de Gras; to Hottah Lake; to mouth of Grandin River, and to Gros Cap	D. v.s.	N. s.		N. s.	0
	Group 11. Coppermine River to Alaska					
	Coppermine, 50 miles east, west and south	D.	N.		s.	—
29.	Basil Bay and 50 miles radius in Coronation Gulf	D. v.s.	N. s.	v.a.	D. s.	+[11]
43.	From Tuktoyaktuk east along the coast to Pearce Point	D. v.s.	I. v.a.		N.	0
	Baillie Island and vicinity	D.	I. a.		I. a.	-
	Aklavik and lower delta of Mackenzie	D. s.	D. s.		I. ×	—
41.	Mackenzie River delta [south to Point Separation], west to Herschel Island and east to Richards Island ...	I. s.	—	a.	D. v.s.	0
	Herschel Island west to Shingle Point	D.	D.		D.	—

* Observer's vote is halved (Table 2).

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1936–37.
Number of observers reporting relative abundance compared with 1935–36

	Eastern Arctic									Western Arctic					
Group No. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	4	10	3	5	2	6	3	33	**57**	1	1	—	1	3	**11**
Decrease	6	3	4	5	—	—	2	20	**34**	5	5	7	6	23	**82**
No change	1	—	2	2	—	—	—	5	**9**	—	—	2	—	2	**7**
	11	13	9	12	2	6	5	58	**100**	6	6	9	7	28	**100**
Lemming:															
Increase	2	8	—	6	—	6	5	27	**64**	4	2	$3\frac{1}{2}$	2	$11\frac{1}{2}$	**43**
Decrease	2	5	—	2	2	—	—	11	**26**	2	3	$2\frac{1}{2}$	2	$9\frac{1}{2}$	**35**
No change	2	—	—	2	—	—	—	4	**10**	—	1	3	2	6	**22**
	6	13	—	10	2	6	5	42	**100**	6	6	9	6	27	**100**
Snowy owl:															
Increase	4	7	3	4	1	6	3	28	**52**	2	1	1	2	6	**32**
Decrease	7	5	5	3	—	—	—	20	**37**	3	1	—	3	7	**36**
No change	—	—	1	5	—	—	—	6	**11**	1	—	4	1	6	**32**
	11	12	9	12	1	6	3	54	**100**	6	2	5	6	19	**100**

Table 3. *State of arctic fox, lemming and snowy owl populations in* 1936–37.
Number of arrows indicating relative abundance compared with 1935–36.

	Eastern Arctic									Western Arctic					
Group No. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	3^{1}	15^{1}	3^{2}	5^{2}	3	19	12^{1}	60^{7}	**45–50**	2^{2}	2^{2}	—	4^{3}	8^{7}	**2–13**
Decrease	6	4^{1}	18^{2}	19^{3}	—	—	2^{1}	49^{7}	**35–41**	9^{2}	19^{2}	21^{3}	7^{3}	56^{10}	**77–93**
No change	1^{1}	—	15^{4}	4^{1}	—	—	—	20^{6}	**12–17**	—	—	6^{3}	—	6^{3}	**5–10**
	10^{1}	19^{1}	36^{4}	28^{3}	3	19	14^{1}	129^{10}		11^{2}	21^{2}	27^{3}	11^{3}	70^{10}	
Lemming:															
Increase	2^{1}	12^{7}	—	10^{2}	—	19	14	57^{10}	**62–75**	4	4^{1}	6^{5}	2	16^{6}	**20–32**
Decrease	2	10^{7}	—	8	3	—	—	23^{7}	**21–30**	5	6^{4}	12^{4}	3	26^{8}	**36–52**
No change	2^{1}	—	—	4^{2}	—	—	—	6^{3}	**4–8**	—	8^{4}	9^{2}	2	19^{6}	**26–38**
	6^{1}	22^{7}	—	22^{2}	3	19	14	86^{10}		9	18^{5}	27^{6}	7	61^{11}	
Snowy owl:															
Increase	4	10^{6}	13^{2}	8^{5}	2	19	12	68^{13}	**48–59**	3^{3}	3^{1}	1^{1}	2^{1}	9^{6}	**8–24**
Decrease	7	10^{6}	21^{2}	14^{5}	—	—	—	52^{13}	**34–45**	7^{2}	2^{2}	—	5^{1}	14^{5}	**24–37**
No change	—	—	2	9^{4}	—	—	—	11^{4}	**6–10**	1^{1}	2^{1}	18^{1}	1	22^{3}	**33–58**
	11	20^{6}	36^{2}	31^{8}	2	19	12	131^{16}		11^{3}	7^{2}	19^{1}	8^{1}	45^{7}	

The index figures in lines 1–3 under each species show the no. of conflicting arrows; in line 4 the no. to be subtracted from the totals in calculating percentages.

Table 4. *Details of disease among sledge dogs*, 1936–37.

Numbers indicate that the full description of an area has already been given and is to be found opposite the corresponding small number in the last column of Table 1.

(*a*) *Disease or epidemic prevalent* (+ on map).

Quebec and Labrador.

Natashquan. "Quite a few dogs died of unknown disease in the fall of 1936."

Romaine. "This year considerably fewer dogs succumbed to disease than last year."

Mutton Bay. "Distemper killed from 60 to 75% of the sledge dogs."

Blanc Sablon. "All sledge dogs in this vicinity had distemper, commencing late in February and still prevalent. Almost all have died with the disease. It spread from the east."

1. *Frenchman's Island.* "During the month of January the south section of the coast was stricken by an epidemic among the dogs, which lasted up to about the middle of March. When the dogs were taken sick they would cough, fall and stay down for about 15 minutes, then get up, go round in a circle about ten times, and go in a straight line very fast. Soon after they would die."

2. *Cartwright.* "A dog epidemic appeared in Cartwright during the early winter and destroyed practically all the teams. It also spread southward, causing destruction to the dogs. The northern teams were spared by prompt measures being taken to stop all teams from this section from going north. The symptoms took different forms: some dogs went mad, others went blind and had distemper, while others would not eat and wasted away. In some cases there appeared to be acute abdominal pain and leg cramp. A larger percentage of dogs died during this epidemic than in any other that has appeared among the dogs."

4. *Georges River.* "A number of dogs have been sick this spring. Symptoms: frothing at the mouth and staggering. Some died but the majority recovered."

5. *Fort Chimo.* "Several sledge dogs are reported to have died."

6. *Sugluk West.* "Epidemic in February and March: violent and painful diarrhoea, loss of appetite. Only fatal in cases underfed previously."

7. *Cape Smith.* "Disease noticed in early winter. Symptoms: contraction of stomach muscles, loss of walking powers."

N.W. Territories.

9. *Whitefish Lake.* "Disease in May. Pus in eyes and nose—especially pups. Also found in lungs."

10. *East end Great Slave Lake.* "Some disease in April and May. Symptoms: running at nose, loss of flesh—no food; death usually follows."

11. *Basil Bay.* "Disease appeared in February and March. Symptoms: large pockets of pusy fluid breaking out almost anywhere on the dog. Most dangerous for young dogs and pups."

Manitoba.

Island Lake. "Practically all sledge dogs died during winter. Heavy discharge from eyes and nose, stomach trouble."

Oxford House. "Sickness amongst the dogs prevailed in the entire district during the winter. Many died."

Pukatawagan. "Great numbers of sledge dogs have died of distemper this spring."

Saskatchewan.

Pine River. "Distemper made great havoc among the dogs of the entire area in early winter."

Clear Lake. "Disease among sledge dogs from July 1936 until December 1936, about 20% of the dogs in this locality died off."

Fond du Lac. "Considerable amount of paralysis in hind legs; blood passed with urine."

(*b*) *Isolated cases of disease* (0 on map, but qualified as below).

Labrador.

3. *Northwest River.* "A few dogs around the Bay suffered from 'dog sickness' but it was not of a violent character here as very few, if any, died from it."

N.W. Territories.

8. *King William Island.* "Two cases of glandus rabies."

Table 4 (*cont.*)

(*c*) *Disease absent* (0 on map. When more than one symbol is given this is stated (2) or (3)).

N.W. Territories.

26 *miles east of Fort Smith.*
Fort Smith district. 60th parallel to east boundary of Wood Buffalo Park and south-eas boundary of Slave River preserve, north-east to Nonacho Lake and south to 60th parallel.
Mouth of Big Buffalo River.
Providence and Hay River (2).
Fort Providence and up Horn River to Horn Mountains.
Fort Providence.
Liard River.
South Nahanni valley and south fork for about 100 miles.
Willow River district, 125 miles down river from Fort Simpson.
Wrigley, Norman and Franklin (3).
Good Hope.
Arctic Red River.
Point Separation and Arctic Red River (2).
[*Cape Perry*, via Aklavik.]

4. Summary

1. This is the second annual report of an enquiry into population trends of lemmings (*Lemmus* and *Dicrostonyx*), the arctic fox (*Alopex lagopus*) and the snowy owl (*Nyctea nyctea*) in the Canadian Arctic. The enquiry was promoted by the Northwest Territories Administration of the Canadian Government, in co-operation with the Hudson's Bay Company, and mapped in the Bureau of Animal Population at Oxford.

2. Replies were received from 111 observers in the North, also from certain Hudson's Bay Company posts outside the Arctic, and the results are shown on maps giving a comparison with the season 1935–36, and analysed in a series of statistics which include allowance for the areas covered by different observers.

3. In the Eastern Arctic there was considerable increase reported in arctic foxes, especially on Baffin Island and the coast of Northern Quebec. Lemmings and snowy owls, which had begun to recover from scarcity in the previous season, showed further well-marked increase in the same region, and also to some extent elsewhere.

4. In the Western Arctic there were very few signs of such recovery among any of the species studied.

5. Details about disease among sledge dogs were also obtained, both from the Arctic and from certain more southerly posts. Several teams suffered heavy losses in the Eastern corner of Quebec Peninsula, while less severe outbreaks occurred along the coast of Northern Quebec. In the Western Arctic there was little disease in the North, but severe outbreaks were reported from Northern Manitoba and Saskatchewan.

6. Information about the numbers of ptarmigan was again received, but reserved for future analysis. The enquiry is being continued.

Reference

Chitty, D. & Elton, C. (1937). "Canadian Arctic wild life enquiry, 1935-36." J. Anim. Ecol. 6: 368–85.

A. E. BOYCOTT

AN APPRECIATION

By E. J. SALISBURY

By the death of Arthur Edwin Boycott, at the early age of sixty-one, science has lost a distinguished pathologist and a naturalist of outstanding ability, whilst, for those who knew him well, there has passed from the scene a rich and scholarly personality whose friendship it was a privilege to enjoy.

The second son of a Hereford solicitor, Boycott was born in a district wealthy alike in its geological diversity and in the variety of its flora and fauna. Moreover, about the time that he was attaining maturity the Woolhope Club was at the zenith of its activity in the study of Natural History. On the excursions of the Club, Boycott, whilst still at the Cathedral School, came in contact with kindred spirits and particularly E. A. Bowles, who interested him in the Mollusca. At the age of seventeen he published a catalogue of the snails of Herefordshire, and this was the prelude to a lifelong interest in the subject of geographical distribution which in later years led to his editing the Roebuck Memorial number of the Conchological Society (1921), in which the data collected by W. Denison Roebuck were embellished by distribution maps, of all the British land and fresh-water Mollusca, which had been prepared by Boycott.

From Hereford Boycott went to Oriel College as a classical scholar and subsequently to Brasenose whence he obtained a first in the Natural Science Honours School. He subsequently went to St Thomas's Hospital and later to the Lister Institute.

From 1912 to 1915 he occupied the Chair of Pathology at Manchester University, where he came in contact with that peerless field naturalist, Charles Oldham. In 1915 Boycott was appointed to the Graham Professorship of Pathology in the University of London, tenable at University College Medical School, and at the same time came to live at Radlett.

In his new environment he quickly became an active member of the Hertfordshire Natural History Society and a regular attendant at its meetings, which were enriched by his gift for discussion and enlivened by his whimsical humour. At this time the H.N.H.S. included amongst its active members Dr Cook, the authority on Radulae, whilst C. Oldham, with whom the writer was privileged to serve as joint Hon. Secretary, was now as distinguished an authority on the Mollusca, especially that critical genus the *Pisidia*, as upon the habits of British birds. Boycott thus enjoyed the stimulus of sympathetic contacts and found time not only to pursue his professional duties and to edit

devotedly for more than a quarter of a century the *Journal of Pathology*, but to extend his studies of the habits and distribution of snails. The latter led him in 1918 to deliver as his Presidential Address to the Hertfordshire Society an account of the fresh-water Mollusca of the parish of Aldenham. This paper is a tribute alike to his industry and scholarship as also to his love of numbered paragraphs and footnotes. Some years later this account was supplemented by the results of further study in a second paper, and his Presidential Address to the British Ecological Society in 1933 was an extension of the same theme.

Boycott's tall figure, lean almost to emaciation, and clear-cut features were no more striking than his colourful personality. A man of strong views strongly held, he regarded any sort of compromise in respect to these as a betrayal of principle, though it were to the detriment of the causes which he espoused. To those who chiefly encountered his prejudices the marked capacity he had of exercising balanced judgement on scientific matters sometimes came as a surprise, whilst the very human and essentially kindly disposition beneath, that never spared itself in the service of others, was apt to remain unsuspected.

Boycott was at his best and happiest when tramping the country, which he loved with a discriminating appreciation, clad in an old suit of clothes and canvas shoes that, as he himself would put it, allowed water to drain away as fast as it had entered, and armed with a snail scoop. Thus equipped, with a tacit agreement to avoid the more controversial topics, he was the most delightful and charming of companions, as ready to learn as to impart, and as ready to apprehend phenomena of which he knew little as those of which he knew much.

Boycott's contributions to pathology were both numerous and distinguished, whilst his biological researches were no less able, but it was perhaps his passion for knowledge and his marked capacity to visualize it as a whole, rather than as so many abstractions, that marked him out from so many of his contemporaries.

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 26, No. 2, August 1938)

This number opens with an appreciation (by E. J. Salisbury) of the character and work of the late Prof. A. E. Boycott.

The scientific contributions include a number of papers on algal ecology. In one of these, E. M. Lind deals with the periodicity of Algae in Beauchief ponds with reference to the seasonal changes in the solutes dissolved in the waters. E. A. Flint gives a preliminary account along similar lines of the periodicity of phytoplankton in Lake Sarah, New Zealand; while M. B. Hyde contributes records of seasonal variations in photosynthesis by the seaweed, *Fucus serratus*, kept under laboratory conditions for a year.

There are two detailed studies of plants in relation to their environment. G. H. Heath and L. C. Luckwill describe the rooting systems of certain heath plants with reference to the stratification and aeration of the soil; and H. G. Wager deals with the growth and survival of plants in the Arctic in connexion with the problem of the origin of *fjaeldmark*. Along similar lines is a short note by G. H. Bates on the characteristics of the plants of grass verges and paths.

On much wider lines is a general account of the island of Pabbay (on the west coast of the Outer Hebrides) by Charles Elton. This deals with the historical and ecological problems and with both flora and fauna.

Two papers on the Potterne Transplant Experiments of the British Ecological Society are contributed by E. M. Marsden-Jones and W. B. Turrill. One of these is the fifth of the biennial reports on the progress of this work, while the second summarizes the results obtained after ten years, 1928–37.

Three other papers deal in detail with habitat factors. W. H. Pearsall continues the papers on the soil complex in relation to plant communities, with a description of the characteristics of British moorland and bog soils having particular reference to their acidity. R. D. Misra gives the results of a detailed study of the edaphic factors controlling the distribution of aquatic plants in the English Lakes. A paper of very general application is one by R. E. Moreau reviewing the bases of climatic classification for biological purposes, with particular reference to East Africa.

Interest in the statistical study of vegetation continues, and in this number, B. N. Singh and K. Das analyse the distribution of weed species on arable land.

Reviews deal with the *Journal of Animal Ecology*, and with recent books on plant ecology.

W. H. PEARSALL.

ECOLOGICAL TERMS

J. Richard Carpenter (1938). *An ecological glossary.* 306 pp. with 12 appendices, including 6 maps. University of Oklahoma Press, Norman, Oklahoma, U.S.A. Price $4.

Mr Carpenter has attempted a compilation of which the rapidly growing study of ecology stands badly in need. That he has not been entirely successful is hardly surprising in view of the many problems with which the whole subject of ecological nomenclature bristles. But he has made a brave attack which will be of undoubted use, and may form the basis of a future more satisfactory work. Many will probably be irritated by the number of minor blemishes which could well have been avoided by more careful checking, and the reader gets the impression that the whole has been put together with too much haste.

Nevertheless, the book brings together into a handy form a great deal of otherwise widely scattered matter; and those who wish to render important service to their subject by ensuring the correct usage of words and avoiding the unnecessary multiplication of synonyms or neologisms will often be saved much time and trouble by referring to it. The reviewer has already had occasion to be grateful to Mr Carpenter. The appendices include some useful tables and maps.

From its nature, ecology can hardly be considered as a single subject that can be confined within its own technical vocabulary relating to forms and phenomena not otherwise described. In the first place, the ecologist must have at his command, and be able to use with precision at least part of the vocabulary of many other sciences. Secondly, many of the terms descriptive of the natural background are words of common speech which may or may not have a clearly delimited meaning, and may lately have suffered technical restriction. The translation of these words into cumbrous Greek and Latin derivatives, which has been the expressed policy of some ecologists, seems in the present state of knowledge merely to add to the synonymy without advancing clarity of expression.

In dealing with most of the technical terms and words of which the common meaning has been restricted, Mr Carpenter has followed the principle of quoting either the meaning attached by the author first using the word or that adopted in a more readily available work, and in each case of giving a reference to the publication. This method has great advantages; but in a rapidly growing science the meaning that becomes more generally adopted may differ from that first proposed, and the recording without comment of several meanings under the same term does not provide a guide to current usage.

Mr Carpenter has, properly, cast his net widely, and the number of synonyms, overlapping terms, and words of ill-defined meaning is remarkable. If the work had no other merits it would have value in bringing into sharp focus the real difficulties that face the research worker who seeks the unequivocal presentation of his results, and the pressing need for ecologists to put their terminological house in order.

C. DIVER.

AN ECOLOGICAL PANORAMA

W. C. Allee & Karl P. Schmidt (1937). Authorized and rewritten edition of **Richard Hesse's** *Ecological Animal Geography* (*Tiergeographie auf ökologischer Grundlage*). 597 pp., many illustrations. John Wiley and Sons Inc., 440 4th Avenue, New York; and Chapman and Hall Ltd., 11 Henrietta Street, Covent Garden, London, W.C. 2. Price £1. 10*s*.

"The principal impulse by which I was directed", wrote Baron Von Humboldt from Potsdam in 1844, "was the earnest endeavour to comprehend the phenomena of physical objects in their general connection, and to represent nature as one great whole, moved and animated by internal forces.... I would therefore venture to hope that an attempt to delineate nature in all its vivid animation and exalted grandeur, and to trace the *stable* amid the vacillating, ever-recurring alternation of physical metamorphoses, will not be wholly disregarded even at a future age." Although no one else has attempted to paint on such a vast canvas as that covered by Humboldt's *Cosmos*, we are coming again into an age when the task of general correlation, the drawing of provisional patterns and the creation of working frameworks that can give scale and proportion to individual surveys by explorers, naturalists and ecologists, is once more becoming respectable, and less liable than it was to the accusation of superficiality in execution, and impatience to reach easy conclusions which will provide satisfactory fodder for University teaching. There have been several attempts in recent years to describe the ecological structure of the animal world against its natural background of vegetation and physical forces. Among these may be mentioned: in German, Dahl's *Ökologische Tiergeographie*; in English, Newbigin's *Plant and Animal Geography*; and in Russian, Heptner's *General Zoogeography*. Hesse's book is perhaps best known, since, in

spite of certain drawbacks, it is in many ways the best-balanced and most comprehensive in its scope. Realizing its value, the two American editors set out to revise and bring it up to date.

It would have been better if they had been content only to translate and add some notes, or else to write an entirely new book with their own ideas in it. For they state that passages with which they disagreed have been intentionally omitted or changed, and the result is that the reader coming fresh to this edition can seldom know, though he can sometimes guess, which is Hesse, and which is Allee or Schmidt. One is reminded somewhat of the old jest about a Limited Company, that it has no body to be kicked and no soul to be damned.

Any reviewer who takes his task seriously must be in a certain difficulty in trying to assess the true value of the book, for in dealing with such a vast field as the authors do they must be expected to have covered the ground unequally. Similarly, the reviewer has to judge rather by the limited sections of the subject that are familiar to him, how far the text is a fair mirror of modern research on ecological animal geography. For instance, the chapter on Polar Regions is notable in containing no references at all to any field surveys done by European expeditions since the War. Yet the results of these dozen or so expeditions that have carried out work on animal ecology have given a very clear picture of the structure of these arctic and subarctic communities, and the results have mostly been published in official British journals of ecology, and (less accessibly) in Scandinavian and Russian expedition results. When one is told that the "purple sandpiper, *Erolia maritima*, of Spitzbergen, has accustomed itself to a plant diet" (which is absurd, as it lives on insects and Crustacea) how much are we to rely upon other facts cited in regions of knowledge of which we know nothing?

It is no excuse for a book which sets out to cover a very large field to say that mistakes are inevitable on account of the largeness of the field. We expect, rather, that an authoritative book will be thoroughly learned and complete. In the present instance, it was obviously impossible for any two authors to cover effectively the whole field without constantly getting out of date before they could master it and write it up. Yet a more organized attempt by many authors would have lacked the coherence which is achieved in many of the chapters.

Turning to more constructive criticism, let us consider the scope of the book, and the range of information and ideas that a student at the University would be likely to acquire from it, that he could not easily acquire by other means. There is a clear distinction made between the kind of ecological animal geography intended in the present treatment, and the type of historical problem that is bound up with long-continued evolution and migration, and the changing major barriers to dispersal, such as sea and land, mountain and desert. A special chapter explains this point and gives examples of discontinuous range and evidence of former extension and movements. The authors are unable to refer to any convenient text-book on this historical aspect, for none exists.

Other early chapters deal with the general limits to animal distribution, illustrated by examples. Although there are a good many rather meaningless sentences, such as "animal life is not tied hard and fast to unalterable values of the conditioning factors", the discussion is well-sustained, interesting especially in making a bridge between ordinary field ecological facts and physiological knowledge, and is easy to read and follow. No one could read this part of the book without finding much information he was quite unaware of, and getting some sense of the drift of American ideas in this phase of ecology.

The major part of the book is concerned with the three great sections of animal habitats and their faunas: marine, fresh-water, and land. Most of the facts that are cited are backed by references at the end of each chapter, and the easy traps which many European ecologists have fallen into in assuming adaptive values for structures and habits, are skilfully avoided; the authors mention in their introduction that in this respect they have differed a good deal from Hesse in their interpretations and objective approach. It is impossible to follow all the sections in detail, but it may be said freely that the whole of it makes interesting, often fascinating reading, and were it not for a lurking suspicion that a good deal of the detail has not been checked back to the original sources, and the fact that the literature is not up to date, one would acclaim it as a worthy follower in the tradition of Humboldt's *Views of Nature*, though not up to the standard of his *Cosmos*.

The student who reads this book will learn of the existence of innumerable curious facts of which he had previously no inkling, and he will never again with any justice be able to ask a harassed supervisor to find him an ecological problem on which he can do research. This book offers him a good many thousand. Would he like to study the effect of surf action on marine molluscs, the food of sand-dwelling worms, the locomotion of plankton, why flounders do not become sexually mature in fresh water, the habits of animals that live in moss, the ecological uses of fat, the influence of snakes on other animals, the occurrence of the burrowing habit, why grasshoppers favour grassland, the occurrence of alpine beetles, or the fauna of caves, or what? Perhaps in stimulating the ecologists to study and clarify all these smaller problems in their larger setting, the authors of this book will have fully compensated for any mistakes or omissions they may have made. I know of no other means of approaching this huge field of information through any book in the English language, and shall certainly draw upon it for many purposes for many years. To an alert reader, the book is worth its high price.

CHARLES ELTON.

HERD AND FLOCK

(1) F. Fraser Darling (1937). *A herd of red deer.* 215 pp., 8 plates, 10 text-figures and 4 maps. Oxford University Press. Price 15*s*.

(2) F. Fraser Darling (1938). *Bird flocks and the breeding cycle.* 124 small pp., 1 photo and 1 text-figure. Cambridge University Press. Price 6*s*.

(1) In the north-west of Scotland lies some of the wildest hill country in the British Isles. On one part of this, an area of 52,000 acres on which about 1300 red deer (*Cervus elaphus*) live almost unmolested, the author spent two years studying the habits and territory and population inter-relations of the deer. He brought to this pioneer investigation a serious purpose borne of a scientific training, and experience in the Imperial Bureau of Animal Genetics in Edinburgh, together with the complete freedom to carry out his research plans that a Leverhulme Research Fellowship afforded. Watching deer at all is a difficult pastime, but to follow them constantly for two years and get to know every bit of the eighty square miles where they live, and the movements and habits of each group of animals, to recognize the different ages and even individuals, and to become sufficiently invisible and unsmellable to see them behaving naturally, requires a tremendous amount of prolonged stalking and waiting, and facility akin to that of the professional deer-stalker who has been brought up to this life. And yet, withal, it is necessary to retain scientific and critical judgement and not to get out of touch entirely with the stream of ecological thought. The following remark is interesting in this connexion: "If you are to develop this quality of sight so that deer and other objects stand out from the hill in your field of vision, not much reading should be undertaken. This seems to alter focal habit, and a hill-side, instead of having depth, becomes merely a flat homogeneous expanse."

The country is described, and then the author's technique and personal reactions to field work. We learn, for instance, that he went barefoot in the summer and thereby greatly increased the awareness of all his senses.

The environment of the deer is described: climate, ground vegetation, the shape of the country, the insect enemies and the parasites of the deer. But, as with all social animals, it is the other deer which form a dominant part of the environment to any individual, and this part of the story occupies most of the book. The style is easy and gives one a real feeling of the country and of the "outlook" of the deer themselves. There is, in addition to scientific enthusiasm and critical judgement, a strong element of aesthetic enjoyment running through, as well as a spontaneous sympathy with wild animals and a desire to communicate this to others.

Fraser Darling finds the social system of red deer to be a matriarchy, with the sexes running in separate herds for most of the year. He mapped the distribution of groups and

their territories, and followed the changes in social and sexual organization through the seasons. The physiological and psychological discussion of these facts must be left to others; but certain very interesting ecological facts also came out of the investigation. It is often assumed that deer in Scotland are kept down by deliberate controlled shooting. In many places the stags are of course shot in some numbers, and the hinds also are thinned out to some extent as a measure of management. But it is very surprising to find how small the biotic potential of the species really is, after allowance has been made for "infant mortality", mortality before breeding, non-breeding females, and so on. The most astonishing thing of all is the evidence that something like 50% of calves are killed during the first five days after birth, when they are temporarily deserted by the mother and are attacked by predators, especially foxes. In other words, a game warden seeking to prevent deer from over-increasing on a national park in Scotland, would find it simplest to encourage foxes. A very similar condition has been claimed by Peter Frechen for the caribou on Melville Peninsula, in Arctic Canada, where he says arctic foxes destroy the young during the first few days after birth. It is most remarkable that half each new generation should be destroyed within five days, in a species such as the red deer, which may live twenty years, and commonly half that much. The whole question seems worthy of a special study, in view of the very marked increase of deer that is taking place now in many parts of the British Isles.

The author lets his observations mostly speak for themselves. The only weak point in the field work seems to be the difficulty of identifying individuals of different classes at a distance. Here the worker has simply to rely on training and practice. There is no rigid proof. And yet it is on this power of distinguishing, and even of recognizing individual deer, that much of the finer observation is built. But the point is honestly met and discussed, and it can be said that without any doubt Fraser Darling has set a new standard for field study of large mammals, a standard which one would like to see extended to African big game and to the ecological-physiological-psychological study of wild mammals generally.

CHARLES ELTON.

(2) There are many things in this book that will come as a relief to the ornithologist in particular. It is, though it should not be, unusual for a book to be written about birds which treats them as subjects for zoological research. In this case it is especially interesting that the thesis is based wholly upon field work, though of course this sets definite limitations to the degree to which many statements are supported or even verifiable. However, even if the author is prone to throw out ideas, constituting a challenge to the laboratory worker to confirm or disprove his conjectures, we can nevertheless be thankful for the stimulation provided. An instance that occurs is the suggestion on page 7 that the cere may function as a photoreceptor conveying impulses that stimulate the pituitary to active secretion. This is the sort of suggestion that is apt to be quoted by subsequent authors as a definite statement, and so the sooner the presence of nerve endings is demonstrated in the cere, the better. Dr Fraser Darling has provided plenty of hard work as well as food for thought.

The first chapter contains a brief recapitulation of what is known about sexual periodicity and the factors which control it, with particular reference to birds. This might perhaps have been a little longer and a little more critical, but the main points, that light and activity have in certain cases been proved to have a connexion with the increase of gonad size, are brought out, and climatic conditions in the north-west of Scotland reviewed in this light.

Chapters 2 and 3 are the most valuable part of the book. The detailed description of the arrival and gradual assumption of the breeding frame of mind, of two species of British gulls, the herring gull (*Larus a. argentatus*), and the lesser black-backed gull (*Larus fuscus affinis*) provide a model for many field observers inasmuch as the main contentions are kept clear and irrelevant details are excluded. The correlation demonstrated between early laying dates, larger clutches and strength of the breeding colony goes a long way to support the author's main argument, which is that in social birds the visual and auditory stimuli provided by the surrounding colony effect an acceleration in the onset of breeding condition. At present both the physiological mechanism to which he refers such phenomena and the observations themselves need verification, but a fruitful field is certainly provided for further research.

It should be remembered that the author is only concerned with the factors which lead to ovulation; the question of how much courtship actions are concerned only with successful fertilization is not discussed. While commending the author for adherence to the main argument, one feels that it would have been interesting to hear how much courtship persisted into the later breeding phases.

The fourth chapter contains brief references to other species in which similar principles may hold good, and indicates many lines that may profitably be followed. It is to be hoped that such an excellent lead as has been given to us in this book will not be neglected either in the field or the laboratory.

H. N. SOUTHERN.

THREE HUNDRED YEARS OF CONSERVATION

C. L. Collenette (1937). *A history of Richmond Park: with an account of its birds and animals.* 164 pp., 5 plates and 1 map. Sidgwick and Jackson Ltd., 44 Museum Street, London, W.C. 1. Price 7*s.* 6*d.*

The planning of national parks is much in people's minds, but we do not hear a great deal about the possibilities of preserving and managing the plant and animal populations of the national parks that have been proposed for this country. A book which gives glimpses of how this has been done in a more or less carefully managed park near London is therefore interesting, even though it deals with a comparatively small area.

One of the difficulties of applying ecology to the successful deliberate balancing of different elements in a national park, will be that game management and conservation have in Great Britain become a body of traditional lore, long before they had a chance to be a science. That is why countries with a shorter history of large-scale wild life management, such as the United States and the U.S.S.R., are so enormously ahead of us in its scientific application. In these remarks, it is of course assumed that such a thing as the management of populations of wild plants and animals is a practical possibility. The policy of letting everything rip, without control, is only possible in very large areas such as the Kruger National Park in South Africa, which can form a little kingdom of wild country chiefly dedicated to faunal preservation.

A few years before his execution, King Charles I resolved to make himself a fine deer park near London. This project he carried out regardless of the opposition of his advisers, and of all those people who owned rights and private property on what is now Richmond Park. This ground, a mixture of waste land, common, and Crown Land, mostly covered with gorse and oakwoods, among which were certain private houses and properties, had long been hunted in by English kings. In the time of Henry VIII it was known as Sheene Chase. After long negotiations, the owners were bought out (rather handsomely), a wall was built, and in 1637 the New Park came into existence, with rangers to supervise the deer. The king had a little hunting, in fact he still hunted there while he was prisoner, before his death.

During the Commonwealth, the Park passed into the hands of the City Aldermen, whose management did not go much beyond an attempt, frustrated by Parliament, to cut down and sell the oaks, and the consumption of venison at City banquets. With the return of Charles II, the Park went back to Royal patronage, under which it was administered by various rangers until 1904, when it came under the control of the Commissioners of Works. During all this time two kinds of deer were kept and more or less carefully managed and protected. The number of fallow deer (*Cervus dama*) was large, varying from about 1300 to 2000 on an acreage of about 2300; red deer (*C. elaphus*) were fewer: from 50 to 200. Since 1904 small game has no longer been preserved for sport; but the deer, reduced now to about 300 and 80 respectively, are still kept and have an important influence on the vegetation, by eating down the seedlings of young trees. From being a more or less private park for the aristocracy to hunt in (the deer were still hunted in the early nineteenth century), the place has become a public resort in which the policy is to encourage most wild birds and animals indiscriminately.

The three dominant factors which have caused changes in the park are the hunting motive, giving place to a wider conservation; the amount of public access; and the inter-relations of

animal life to the vegetation. There are some curious points unearthed by the author's patient research into archives, and his field knowledge of the park conditions and life. The deer population fluctuated somewhat, but most of the time seems to have kept a very high level without harm. The herds were added to from time to time, were often fed in winter, and in the early days the oaks are thought to have been pollarded to give browse to the deer in times of scarcity. Protection was stringent, and no doubt enemies, such as foxes, were discouraged. The only recorded epidemic was in 1886–7. As a result of this high density, the deer have kept the area comparatively open, while neighbouring commons are grown with scrub.

Rabbits must have aided this seedling tree destruction, for in 1904 when the Government took over management, 2400 rabbits were destroyed. After this relief from rabbit pressure it was noticed that many young birches began to grow up. In 1934 some New Forest ponies were introduced, and are breeding successfully. However, there are a good many plantations that the deer and ponies cannot enter. Deer also destroyed reeds introduced for the water-fowl, and part of each of the two larger ponds is now separated as a bird sanctuary.

A curious incident was the introduction of wild turkeys probably in the reign of George I. There were as many as 3000 of these birds, which ate the acorns, were also artificially fed, and afforded royal sport when they were chased by dogs and treed and shot. This turkey population died out during the nineteenth century. The swan is now regarded as a pest through its attacks on other water-fowl, although it is swans that give the earliest record of game management in the British Isles. A molecatcher was kept to prevent horse-riders from having accidents.

The history of access is given: a brewer called John Lewis fought and won a test case, after which the public was admitted for the first time in fairly large numbers (1758), but only over ladders on the walls, so that the deer should not get out. From the early nineteenth century onwards some domestic animals were also kept in the Park. One result of excessive human visitors is the beating down of dead bracken in which certain birds make their nesting sites. The pollution of Beverley Brook has mostly stopped the fine annual run of young eels to the ponds that used to be observed. But the ponds themselves contain various other fish.

The first part of the book has most of the historical material. Part 2 is given up to the fauna, chiefly birds, for which many valuable records are made under the various species. One of the modern problems is evidently what should be classed as vermin. Foxes persist in spite of killing (116 were destroyed in six years), there are five badger earths, the grey squirrel is permanent, although 200 were shot in five years. And a small population of pheasants and partridges hangs on without any special assistance. There must be innumerable questions that could be studied by ecologists in Richmond Park, and that would throw light on the inter-relations of the 80 regular resident or visiting birds, the dozen or so mammals, not to speak of the thousands of other animal species. It is to be hoped that this monograph will give a useful frame into which further studies can be fitted. Still more one wishes that the future large national parks should have faunal surveys done now before they are handed over to regional committees armed with extraordinary powers.

CHARLES ELTON.

IMPROVED PHENOLOGY

H. C. Gunton (1938). *Nature study above and below the surface: a bridge between amateur and professional.* With a preface by C. B. Williams. 134 pp., 18 text-figures and photos. H. F. and G. Witherby Ltd., 326 High Holborn, London, W.C. 1. Price 7*s.* 6*d.*

This book will be very useful to ecologists because it gives such an excellent account of modern methods of compiling phenological records, together with an analytical discussion of the results, illustrated with numerous diagrams and tables. Much of it is chiefly entomo-

logical in scope but the subject is well covered and includes mention of most recent researches of interest to field naturalists. An important feature is the way in which the book suggests useful lines of work for the amateur and stresses the need for collaboration.

The book is well produced and generally accurate although it contains a few misprints (e.g. p. 31, *phlaes* for *phlaeas*, Nymphauds for Nymphalids, *paleacia* for *paleacea*) and several misleading statements (e.g. p. 29, "many moths, as well as butterflies, are attracted to blossoms, and feast on their pollen"). These are, however, but small blemishes and the book should be well received.

B. M. HOBBY.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology,* Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free, (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, F. C. Evans and B. M. Hobby.

1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine and brackish

See also **155, 185, 288**

143. Moore, H. B. and others (1937). "Marine fauna of the Isle of Man." (Reprinted from Proc. Liverpool Biol. Soc.) University Press of Liverpool, 175 Brownlow Hill, Liverpool. Price 2*s*. (2*s*. 6*d*. post free). 293 pp. and 3 charts.

Lists of all invertebrates and fishes known to have been found within a radius of 5 miles from the shore of the island. Including bibliography. Notes on seasonal occurrence, depth and type of habitat are incomplete. Some short lists of species characteristic of different habitats are given. (See also **288**.)

144. Wells, A. Laurence (1938). "Some notes on the plankton of the Thames Estuary." J. Anim. Ecol. 7: 105–24.

Collections of phyto- and zooplankton (mostly at Southend-on-Sea) were made between November 1933 and April 1937. The results are described against the general background of Thames Estuary sea-food industries, which include cockle, oyster, whitebait, and shrimp, all depending mainly upon plankton for their basic resource. Special account is given of seasonal variation in the diatom and Copepod community, and to quantitative changes with the tidal cycle. The methods of sampling are described, many useful ecological notes are given on various groups studied, and two useful charts showing the general distribution of types of sea-bottom and important animals within the Estuary.

145. Raitt, D. S. (1937). "The benthic Amphipoda of the north-western North Sea and adjacent waters." Proc. Roy. Soc. Edinburgh, 57: 241–54.

This order is an important element in the food of marine fish. Analysis was done (*a*) of bottom sampler material taken between 1922 and 1930 (of which a distribution map is given for the numbers of samples), which yielded 1605 specimens of Amphipods, of 79 species; (*b*) 69 haddock stomachs, of which 42 contained Amphipods: 1599 specimens and 47 species. The average frequency of specimens of this order in bottom samples was about 540 per 100 sq. m. for the Coastal zone, 400 for the Offshore zone, and 180 for the North-eastern zone. A complete list of species and their general distribution in the area is given, and remarks on the species composition in different zones. *Ampelisca* (of which eight species were taken) formed the commonest type: 55 % of specimens in the grab samples, and 45 % in the haddock stomachs. The survey therefore establishes *Ampelisca* as one of the key-industry animals in bottom-feeding fish production, more particularly affecting post-larval and adolescent fish.

146. Forrest, J. E. (1938). "Notes concerning some animals obtained from three German warships recently salved at Scapa Flow, Orkney." Scot. Nat.: 3–8.

These vessels were sunk in 17 fathoms of water, where they remained for 16 years. The fairly extensive list of species includes only those which remained after the vessels had been scraped, but nevertheless seems to indicate a great variety of marine life in the seas around the Orkneys.

147. McMillan, N. F. (1937). "Marine Mollusca at Belan Fort, Foryd Bay, Caernarvonshire." North Western Nat. 12: 401–2.

A list of species from one small area.

148. Fisher, N. (1937). "Nudibranchs from N.E. Ireland." Irish Nat. J. 6: 200–2.

List of sea-slugs with good habitat notes.

149. Lynn, M. J. (1936). "The scarcity of *Zostera marina* (slitch, eel-grass or grass-wrack) in Strangford Lough." Irish Nat. J. 6: 107–17.

Describes the diminution of *Zostera* locally, with a general account of the decrease of the plant elsewhere. Causes of decrease are analysed: no single one can be given sole responsibility.

(*b*) Freshwater

See also **160, 161, 162, 164, 178, 186, 188, 192, 196, 197, 283, 287**

150. Macan, T. T. (1938). "Evolution of aquatic habitats with special reference to the distribution of Corixidae." J. Anim. Ecol. 7: 1–19.

Survey of all species of lesser water-boatmen found in the English Lake District. Species classified into groups according to their habitat, and position of this habitat in the succession series from low to high organic content of soil previously worked out by Pearsall. There is a special group in high tarns.

151. Wilson, G. (1937). "Notes on mosquitoes of Belfast." Irish Nat. J. 6: 166–7.

Eight species, with some habitat notes.

152. Kimmins, D. E. (1938). "British Ephemeroptera, Plecoptera and Trichoptera in 1936." J. Soc. Brit. Ent. 1: 202–9.

A valuable addition to knowledge of the distribution of these Orders.

153. Cowley, J. (1938). "Notes on British Odonata in 1937." Entomologist, 71: 108–10.

Dates of occurrence in Surrey and Sussex.

154. Hammond, C. O. (1938). "The dragonflies of Byfleet." Entomologist, 71: 84–6.

Habitat notes of 23 species.

155. Reid, D. M. (1938). "Forms of *Gammarus* from Ireland." Nature, 141: 690.

G. duebeni, usually a brackish-water species, was found generally distributed throughout Ireland in rivers and freshwater loughs, in waters of widely varying *p*H. *G. pulex* was reported only from Lough Erne.

156. Smith, S. H. (1937). "Distribution of the crayfish (*Astacus pallipes*)." Naturalist, 17.

Notes on Yorkshire localities.

157. Fry, A. H. (1938). "The upper Avon and its water meadows." Avon Biological Research, Annual Rep. 1936–37, 20–8.

Describes the course of the river through different geological formations and soils, and gives a classification (with map based on Land Utilization Survey) of various pasture types in the Avon above Salisbury. The subject has a relation to fisheries through silting and food supply and water.

(*c*) Land

See also **153, 154, 200, 210, 233, 283**

160. (London Natural History Society) (1938). "The survey of Limpsfield Common." London Nat. for 1937: 46–66.

Preliminary studies of the ecology of a Surrey common, organized by a committee of the Society, with the help of various workers. The main vegetation types have been mapped and soil acidities determined. Lists of species include bryophytes, fungi, lichens, plant galls, Diptera, Amphibia, reptiles, birds and mammals. Careful habitat notes are given for the species. "The survey of Limpsfield Common aims at a knowledge, as complete as possible, of the fauna and flora of the area, its numbers of individuals, their fluctuations and the causes, their interrelations, and their habits as influenced by the area and its conditions. The basis of such a study must be correctly identified plants and animals to enable past, present and future knowledge to be correlated."

161. Fitter, R. S. R. (1938). "Mammal, etc., recording in 1937." London Nat. for 1937: 92–3.

A list of 42 mammals, five reptiles, and six Amphibia, recorded within 20 miles of the centre of London since 1900. Most of them (except for many of the bats) have been found also since 1920.

162. Homes, R. C. (ed. by) (1938). "Birds in the London Area, 1937. Report on bird-life within twenty miles of St Paul's Cathedral." London Bird Report for 1937: Suppl. to London Nat. pp. 1–34.

Besides the usual type of list with local records of occurrence, there are special notes upon certain species: magpie, which avoids densely populated areas; red-backed shrike, with a scattered distribution which is discussed; coot, of which large flocks come into the area from outside in the autumn; pied wagtail, which had a roost of sometimes over a hundred birds in Richmond Park. A complete census of coots, great-crested grebes, and all species of ducks was done on 18 December 1937, on a number of the main pieces of water round London. There are also notes on migrants and upon ringing work.

163. Tully, H. (1938). "Some birds on the north Northumberland coast in June and July, 1937." Vasculum, 24: 40–5.

Compares observations with those recorded in works by Chapman (1907) and Bolam (1912), and suggests that there may have been changes in the habits of several Northumberland species.

164. Frank, A. Stanley, Flintoff, R. J., Green, J. & Patterson, J. (1937). "Notes on the Hole of Horcum, Saltersgate, North Yorkshire. 3. The birds of the District." North Western Nat. 12: 125–40.

The birds are listed under general habitats (woods, moorland, heaths, marsh, etc.) instead of in systematic order, and good habitat records are given for each, with seasonal variations.

165. Steel, W. O. (1938). "Insect life in a dying willow." London Nat. for 1937: 68–9.

Notes on eleven species, in wood and under bark.

166. Hayhurst, H. (1937). "Insect infestation of stored products." Ann. Appl. Biol. 23: 797–807.

A survey of insects found on the London, Midland and Scottish Railway.

167. Wilson, G. Fox (1938). "Pests of commercial ornamental plants." Scientific Horticulture, 6: 102–16.

The chief forms dealt with are: stem or bulb eelworm (*Anguillulina dipsaci*), already recorded from over 300 species of plants; fern or leaf eelworm (*Aphelenchoides olesistus*) causing leaf infection of ferns, also of many other plants; Tarsonemid mites, on the under-sides of leaves of various species; rhododendron bug (*Leptobyrsa rhododendri*); glasshouse leaf-hopper (*Erythroneura pallidifrons*) sucking under-sides of leaves; rhododendron white fly (*Dialeurodes chittendeni*), whose honeydew on upper leaf surfaces encourages certain moulds; knapweed aphis (*Macrosiphum jaceae*), on cornflowers (*Centaurea*); tulip aphis (*Anuraphis tulipae*), attacking bulbs of iris and tulip, and corms of *Gladiolus*; scale insects and mealy bugs in a large number of plants; rosy rustic moth (*Hydroecia micacea*), a stem miner of wild plants, sometimes attacking *Antirrhinum* and *Dahlia*; swift moths (*Hepialus*), attacking roots of many species; carnation tortrix moth (*Tortrix pronubana*), leaf-rolling and bud-eating larvae, polyphagous; vine weevil (*Otiorrhynchus sulcatus*), larvae on roots, etc., and adults nocturnal on leaves of various kinds of plants; violet midge (*Dasyneura affinis*), leaf-rolling; fruit flies on *Berberis*, *Cotoneaster*, *Pyracantha* and *Rosa*. The need for constant vigilance is stressed, as the polyphagous habits of many pests enable them to change from wild plant hosts to cultivated ones. Methods of control for different pests are given, and an appendix lists the chief plant hosts and their known pests.

168. Guichard, K. M. (1938). "Aculeates on the Norfolk coast." London Nat. for 1937: 71–2.

27 species of bees and wasps listed from *Psamma* sand dunes.

169. Faris, R. C. (1936). "Records of some bees, wasps, and ants from County Cavan, in 1933." Irish Nat. J. 6: 143–5.

Includes some ecological notes.

170. Niblett, M. (1937). "Some observations on plant-galls caused by gall-wasps (Cynipidae)." Proc. S. Lond. Ent. Nat. Hist. Soc.: 61–8.

An account of abundance, host-plants and galls, chiefly from observations made in Surrey.

171. Donisthorpe, H. St J. K. (1938). "A preliminary list of the Coleoptera of Windsor Forest." Ent. Mon. Mag. 74: 21–7, 67–77, 115–26.

172. Kaufmann, R. R. U. (1937). "Investigations on beetles associated with carrion in Pannal Ash, near Harrogate. II and III." Ent. Mon. Mag. 73: 227–33 and 268–72.

173. Stelfox, A. W. (1937). "Notes on the distribution in Ireland of the long-horn beetles, *Strangalia aurulenta*, *S. quadrifasciata* and *S. armata*." Irish Nat. J. 6: 156–8.

Armata has the widest distribution, while the other two are confined to the southern and south-eastern counties. The three species are illustrated.

174. Fordham, W. J. (1937). "Mole's nest beetles in East Yorkshire." Naturalist: 265–7.

Analysis of the beetle fauna of over 100 mole nests examined between 1913 and 1922.

175. Stanley-Smith, F. (1937). "*Cosmia* (*Xanthia*, *Mellinia*) *ocellaris*, Brkh." Proc. S. Lond. Ent. Nat. Hist. Soc.: 73–9.

A useful contribution to the knowledge of the life-history of this rare moth. The larvae feed in the catkins of poplar which they probably desert later in order to bore into the high leaf buds.

176. Klimesch, J. (translation by **Jacobs, S. N. A.**) **(1937).** "Some remarks on the genus *Nepticula*, Z." Proc. S. Lond. Ent. Nat. Hist. Soc.: 92–107.

An account of the biology of these minute leaf-mining moths, with notes on collecting, breeding and mounting.

177. Otter, G. W. (1938). "On the morphology of the larvae of three species of Cecidomyidae (Diptera) from knapweed (*Centaurea*) flowers." Trans. R. Ent. Soc. Lond. 87: 39–68.

The species described (*Lestodiplosis miki*, *Clinodiplosis cilicrus* and *Dasyneura miki*) play a comparatively small part in the economy of the insect population in the flowers of *Centaurea nigra*.

178. Oldroyd, H., Parmenter, L. & Pugh, C. H. Wallace (1938). "Dolichopodidae (Dipt.) from Silchester Common (Berks.)." J. Soc. Brit. Ent. 1: 232–3.

27 species were obtained along the banks of a stream, mainly in boggy places. The most abundant species were *Dolichopus popularis*, *Hercostomus nigripennis* and *Gymnopternus aerosus*.

179. Thomas, I. (1938). "On the bionomics and structure of some dipterous larvae infesting cereals and grasses. III. *Geomyza* (*Balioptera*) *tripunctata* Fall." Ann. Appl. Biol. 25: 181–96.

Cereals and grasses were preferred in the following order: (1) *Lolium perenne*, (2) *L. italicum*, (3) wheat, (4) barley, *Poa trivialis*, *Dactylis glomerata*, (5) *Cynosurus cristatus*, oats, (6) *Festuca rubra*. Three parasites were bred: *Phaenocarpa livida*, *Chasmodon apterous* and *Stenomalus* sp.

180. Harrison, G. Heslop (1936). "The Psyllidae, or jumping plant-lice, of Northumberland and Durham." Trans. Northern Nat. Union, 1: 217–28.

List of species with good habitat notes, including host plants, and indication of distribution of the species abroad. It was found that a great many species remain on their host plant during winter, sheltering at its base and on the lower twigs.

181. Harrison, G. Heslop (1938). "Observations on the British Psyllidae. II. Notes on the *Salix*-feeding Psyllidae." Ent. Mon. Mag. 74: 8–11.

Mainly host-plant range.

182. Dallas, J. E. S. (1938). "*Atypus affinis* Eichw. in the London District." London Nat. for 1937: 24–5.

Distribution of this trap-door spider in sandy heaths round London (it was found exceptionally on chalk grassland). It is thought that increased trampling by people is destroying its colonies.

183. Waterson, A. R. & Quick, H. E. (1937). "*Geonemertes dendyi*, a land Nemertean, in Wales." Proc. Roy. Soc. Edinburgh, 57: 379–84.

This is apparently the first record of a land Nemertean worm established in the temperate climate of Europe. Internal and external characters are described. The worms are active at night, and are found in damp shady places near streams or trees. Eggs were found in March, but were laid in captivity in October, November and April. Previously known from West Australia, and a glasshouse in Germany, it has now been found around Swansea, associated with land planarians (*Rhynchodemus terrestris*) and a list of Mollusca which is given. It has been found in the same area in three successive years.

(*d*) Small islands

184. Warwick, T. (1938). "Notes on mammals of the isles of Barra, Mingulay, and Berneray, Outer Hebrides." Scot. Nat.: 57–9.

Notes on two aquatic and five land mammals. Most of the notes are on *Apodemus hebridensis* (collected on Barra and Berneray, and said to occur on Mingulay). Other species noted on land were *Sorex minutus*, *Rattus norvegicus*, *Mus musculus* (living wild), and rabbits.

185. Southern, H. N. (1938). "A survey of the vertebrate fauna of the Isle of May (Firth of Forth)." J. Anim. Ecol. 7: 144–54.

The first part of this paper describes the occurrence, dimensions (including weights) and parasites of the house mouse (*Mus musculus*) living out of doors. The second part gives counts of the breeding pairs of land, shore, cliff and ternery, and predatory birds, with a general description of the island and a map showing vegetation zones. There are also some notes on non-breeding birds. There have been changes in numbers in several species in recent years. The most striking is in the herring gull (*Larus argentatus*), from 58 pairs in 1924 to 455 in 1936 (the date of the census given here).

186. Harrison, J. W. Heslop & Peacock, A. D. (ed. by) (1938). "The natural history of the Island of Raasay and of the adjacent Isles of South Rona, Scalpay, Longay and Fladday." Scot. Nat. (for pages see below. Earlier parts noticed in J. Anim. Ecol. (1938) 7: 167–8, No. **38**).

"VIII. Notes on the bird life of the island of Raasay, Inner Hebrides." By **G. W. Temperley.** Pp. 11–27.

The history of the island has greatly affected the bird life. Before 1852 the Macleods who owned it maintained a large amount of natural game, and the island was densely populated by people. After 1852 a new order evicted 94 families in order to make the island into a sheep ranch, and it reverted to rough grazings. Eventually it passed into a regime of intensive game preservation, with the introduction of partridge and pheasant and destruction of enemies of game birds (e.g. hen-harrier, peregrine, merlin, rook, heron) and new plantations were made. After 1912 the island was used for ironstone mines and game preservation declined. After the War the mines were closed and the island passed into the hands of the Board of Agriculture for Scotland. During the post-1912 period game-birds and animals decreased greatly, and deer and grouse are now very scarce, but crows are abundant. A full list of birds is given, with habitat notes and general indications of numbers and breeding status.

"IX. The Ephemeroptera, Plecoptera, Megaloptera, Neuroptera and Mecoptera of Raasay and the adjacent islands of South Rona, Scalpay, and Pabbay." By **J. W. Heslop Harrison.** Pp. 28–30.

30 species recorded, with some general habitat notes for some of them.

"X. The aquatic Coleoptera of Raasay and of the adjacent islands of South Rona, Fladday, Scalpay, Longay, and Pabbay." By **G. Heslop Harrison.** Pp. 60–4.

42 species of water beetles recorded (43 have been recorded by another worker for Skye). General habitat notes and locations are given for some species. *Aulonogyrus striatus*, a Gyrinid new to the British Isles, and usually considered a Mediterranean species, was taken on Raasay in a low-lying loch.

187. Harrison, J. W. Heslop (1937). "The Lepidoptera of the Isle of Raasay and of the adjacent islands of Scalpay, South Rona, Fladday, and Longay." Proc. Univ. Durham Phil. Soc. 9: 305–28.

Results of field expeditions in 1934–36 to these islands of the Inner Hebrides. 329 species were collected, and a certain amount of habitat information is recorded.

188. Harrison, J. W. Heslop (1937). "The Trichoptera of the Isle of Raasay and of the adjacent islands of South Rona and Scalpay." Proc. Unvi. Durham Phil. Soc. 9: 329–31.

45 species, with localities and a few habitat notes.

189. Harrison, J. W. Heslop (1937). "The Cecidomyidae or gall gnats of the Isle of Raasay and of the adjacent islands of Scalpay, Rona, and Longay." Proc. Univ. Durham Phil. Soc. 9: 332–5.

46 names recorded, with host plants.

190. Harrison, J. W. Heslop (1937). "The Hymenoptera of the Isle of Raasay and of the adjacent islands of Scalpay, South Rona, Fladday, and Longay." Proc. Univ. Durham Phil. Soc. 9: 336–40.

20 bees, five ants, ten wasps, one Chrysid, four Ichneumonids, 13 Cynipids, four sawflies.

191. Harrison, G. Heslop (1937). "The Psyllidae or jumping plant-lice of Raasay and of the adjacent islands of Rona, Fladday, Scalpay, Longay, and Fladday." Proc. Univ. Durham Phil. Soc. 9: 341–4.

Four summers' collecting produced 32 species, for which good host-plant and habitat records are given.

192. Harrison, J. W. Heslop (1937). "The Hemiptera-Heteroptera of Raasay and of the adjacent islands of South Rona and Scalpay." Proc. Univ. Durham Phil. Soc. 9: 346–51.

76 species with some general habitat notes.

193. Harrison, J. W. Heslop (1938). "The Rhopalocera of the islands of Coll, Canna, Sanday, Rhum, Eigg, Soay, and Pabbay (Inner Hebrides), and of Barra, Mingulay and Berneray (Outer Hebrides)." Entomologist, 71: 18–20.

Records of sixteen species. Further reference in *id.* 70: 1–4.

194. Harrison, J. W. Heslop (1938). "A contribution to our knowledge of the Lepidoptera of the islands of Coll, Canna, Sanday, Rhum, Eigg, Soay and Pabbay (Inner Hebrides), and of Barra, Mingulay and Berneray (Outer Hebrides)." Proc. Univ. Durham Phil. Soc. 11: 10–23.

Lists of many species with a few general habitat notes.

195. Dowdeswell, W. H. & Ford, E. B. (1938). "The Lepidoptera of Cara Island." Entomologist, 71: 82–3.

Nine additional species to the previously recorded 45. Ten butterflies and 44 moths.

196. Balfour-Browne, F. (1938). "The aquatic Coleoptera of the Outer Hebrides. Second paper." Scot. Nat.: 33–46.

Beetles collected on the island of Barra in June and August increase the total number of aquatic species for the island to 42, and the list for the Outer Hebrides generally to 63. There are some habitat notes and a complete list of species.

197. Walker, J. J. (1938). "On the Coleoptera, etc., of the Faroe Islands." Ent. Mon. Mag. 74: 77–82

156 species of Coleoptera as compared with 232 recorded from the Shetlands and 141 from Iceland.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

198. Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1938). "The handbook of British Birds. Vol. 1 (Crows to fly-catchers)." H. F. and G. Witherby, Ltd., 326 High Holborn, London. Price £1. 1*s*. per vol. for subscribers to all five volumes; £1. 5*s*. for single volumes.

A partly rewritten edition containing much new matter, especially on the ecological side, illustrated with small coloured plates of every species in various states of plumage. Indispensable for all field ecologists dealing with birds.

199. Longfield, C. (1937). "The dragonflies of the British Isles." 220 pp. and 260 illustrations. F. Warne and Co., Ltd., Bedford Court, Bedford Street, London, W.C. 2 and 381 Fourth Avenue, New York, U.S.A. Price 7*s*. 6*d*.

Concise reference book for the group, with keys for identifying fresh specimens in the field (but not entirely adequate for preserved ones). Includes useful summary also of many ecological characteristics. (Reviewed in J. Anim. Ecol. (1938) 7: 162.)

200. Lal, K. B. (1938). "On the immature stages of some Scottish and other Psyllidae." Proc. Roy. Soc. Edinburgh, 57: 305–31.

An important new guide to the immature stages of 13 species of jumping plant-lice. Most of the species described are on trees and shrubs: alder, ash, box, hawthorn, *Pyrus* spp., sallow, buckthorn, *Eucalyptus*; a few also on herbs: nettle, willow-herb.

201. Richards, O. W. (1938). "A species of *Sphaerocera* (Diptera, Sphaeroceridae) new to Britain." Proc. R. Ent. Soc. Lond. B, 7:127–30.

Includes a key and notes on *S. micropyga*, *S. crenata*, *S. paracrenata* and *S. falcozi*, of which the third has not hitherto been recorded from England. All have hitherto been rare in collections, probably because they are inhabitants of the nests of birds and mammals situated in very damp places.

202. Edwards, F. W. (1938). "British short-palped craneflies. Taxonomy of adults." Trans. Soc. Brit. Ent. 5: 1–168.

Keys, descriptions and distribution of the 214 British species. Used in conjunction with H. Audcent's paper on the larger species (1932, Trans. Ent. Soc. S. Engl. 8: 1-34), should make it possible to identify any British "daddy-longleg."

203. Edwards, F. W. (1938). "On the British Lestremiinae, with notes on exotic species. 1. [2, 3]. (Diptera, Cecidomyiidae.)" Proc. R. Ent. Soc. Lond. B, 7: 18–24, 25–32, 102–8.

This subfamily has hitherto remained one of the least known groups of British Diptera, no doubt because the species are small and inconspicuous, while few or none of them are of economic importance and (in contrast to the Cecidomyiinae) none of them is a gall-maker. The British material examined consisted largely of adult specimens captured either on windows or in woods and about old logs. Keys and figures are given.

204. Emden, F. van (1938). "On the taxonomy of Rhynchophora larvae." Trans. R. Ent. Soc. Lond. 87: 1–37.

An important paper giving keys to genera and many species of weevils, with considerations of their affinities.

205. Kerrich, G. J. (1938). "A revision of the British species of the genus *Hygrocryptus* Thoms. (Hym., Ichneumonidae, Cryptini)." Trans. Soc. Brit. Ent. 5: 169–77.

Includes key to the six British species.

206. Benson, R. B. (1938). "A revision of the British sawflies of the genus *Empria* Lepeletier (Hymenoptera, Symphyta)." Trans. Soc. Brit. Ent. 5: 181–98.

Includes keys and distribution of the thirteen British species.

207. Sherborn, C. D. & Tams, W. H. T. (1938). "Generic, trivial and specific names." J. Soc. Bibl. Nat. Hist. 1: 130.

General ignorance prevails as to the meaning of these three terms. In *Felis leo*, *Felis* is the generic name, *leo* the trivial name, and *Felis leo* the specific name.

208. Jobling, B. (1938). "The cardboard cell method for the mounting of insects and their parts." Proc. R. Ent. Soc. Lond. A, 13: 55–7.

The cell method is generally used for mounting large specimens, when it is necessary to obtain a permanent microscopic preparation without any distortion of the form by pressure of the cover-glass. The technique which is described here differs from others in the use of cardboard rings instead of those made of glass or metal.

209. Drabble, H. (1937). "Plant ecology." 142 pp. and 12 plates. Edward Arnold and Co., Ltd., 41 Maddox Street, London, W. 1. Price 7*s.* 6*d.*

A convenient and concise textbook describing the main British plant associations (with photographs) and with diagrams showing succession, and a short bibliography. The animal ecologist will find this book useful in any attempt he may make to understand the biotic community.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **144**, **150**, **182**, **186**, **242**, **253**, **259**, **265**, **267**, **271**

210. Nelmes, E. (1938). "A survey of the distribution of the wood ant (*Formica rufa*) in England, Wales and Scotland." J. Anim. Ecol. 7: 74–104.

A comprehensive enquiry aimed at mapping all known records of wood ants in Great Britain. Maps for England and Wales, and for Scotland are shown separately, and the former is overlaid on a map giving general soil character, as judged from the distribution of geological zones and glacial drift. Allowance being made for the different areas covered by various soil types (determined by planimeter), frequencies of ant records are worked out, and show a very marked relation between wood ants and sandy or non-calcareous soils. They also tend to come on well-drained places. The Bagshot sands in southern England are one example of high density of colonies on non-calcareous sand. Chalk and limestone have few colonies. This monograph is valuable, not only in giving these correlations, and a full list of detailed localities and references to all published records, but also in providing a rough guide to the distribution and areal importance of different soil formations in England and Wales. Further factors mentioned as influencing wood ant distribution are woodland distribution, tree felling, light intensity, fires, and game preservation. The last factor results both in destruction of nests and in the deliberate introduction of ants to new localities.

211. Thomas, D. C. (1938). "Report on the Hemiptera-Heteroptera taken in the light trap at Rothamsted Experimental Station, during the four years 1933–1936." Proc. R. Ent. Soc. Lond. A, 13: 19–24.

A 300-candle power electric light about 3 ft. 6 in. above the ground was in continuous use. The trap was fitted with a series of eight killing-bottles, changed automatically at intervals during the night so as to provide evidence of the time of flight of particular species. Capsidae were by far the most abundant Heteroptera to come to light both in numbers of species and of individuals (95% out of a total of 1486). This period from the end of June to the middle of September gave the greatest numbers, but does not correspond very well with the observed occurrence of these species in the field and may possibly be accounted for by diminished activity of male Capsidae after copulation. The Corixidae, Nabidae and Lygaeidae taken were mostly females, the Capsidae mostly males.

212. Edwards, F. W. (1938). "Notes on the Mycetophilidae (Dipt.) obtained by Dr C. B. Williams in a light-trap at Harpenden, Herts." J. Soc. Brit. Ent. (1): 199–202.

Exact records were kept of the climatic conditions and also of the period of the night when the insects were caught. Flies of the subfamily Sciarinae predominated, and by far the greater proportion consisted of females. The species most constantly captured was *Sciara brunnipes*, which has a well-marked flight period in the early part of the night, also some slight indication of another flight at dawn.

213. Woodhill, A. R. (1938). "Salinity tolerance and *p*H range of *Culex fatigans*." Nature, Lond., 141: 920.

Generally regarded as a fresh-water mosquito, this species was bred in the laboratory in sea water of various dilutions. Larvae would not develop normally in a salinity greater than 10 g. per mille. Pupae appeared extremely resistant when transferred from low to high salinity. *p*H within the limits of 4·2 and 9 had no effect on development.

214. Fraenkel, G. & Pringle, J. W. S. (1938). "Halteres of flies as gyroscopic organs of equilibrium." Nature, Lond., 141: 919–20.

The anatomical arrangement of the sense organs at the base of the halteres is such as to resist the forces set up by the vibration of these organs. Experimental evidence further supports the balancer theory and lends no support to the idea that the halteres have a purely stimulatory function.

215. Watson, G. I. (1938). "The jump of fleas." Nature, Lond., 141: 923.

A flea after jumping off turns and travels tail-first through the air, thus placing the heavy end foremost. On landing, the flea faces the direction from which it has come. "If the landing place proved uncongenial, I suppose nothing could get away more quickly than a flea, already facing as it is the way it wishes to return."

216. Mellanby, K. (1938). "Activity and insect survival." Nature, Lond., 141: 554.

Female bed-bugs (*Cimex lectularius*) survived on an average 134 days of starvation when not disturbed, but died if forced to run about for 7 days of starvation. Differences in technique thus probably account for previous range of results found by various investigators. "Field conditions" which affect activity will influence longevity of bed-bugs.

217. Fraser, F. C. (1938). "*Vanessa atalanta* hibernating in Hampshire." Entomologist, 71: 86.

In upper rooms of an old house in December.

218. Warren, B. C. S. (1938). "The flying-habits of butterflies when paired." Entomologist, 71: 114–17.

Confirmation of Donzel's theory that the flying habit is the same in all species of a genus. The female flies in the Satyridae; both sexes fly alternately in four species of Argynnids, in other species the female does; in the "Coppers" the female, in the "Blues" the male flies. In the Pierids the male usually flies, in the Hesperidae it is the female.

219. Rippon, C. (1938). "*Asteroscopus nubeculosa*." Entomologist, 71: 120.

The emergence or not of any particular pupa of this moth in a particular March is determined the previous autumn.

220. Walsh, G. B. (1938). "Some relations of British Coleoptera to their environment." Trans. Soc. Brit. Ent. 5: 199–222.

Rate of loss of water is greater in dead beetles than in living ones, is proportional to time of exposure, is increased by wind and dependent upon temperature and the size of the elytra. Brachelytra show little resistance to drought conditions and are almost invariably found in a damp environment. Beetles where the elytra are in a fixed position close to the body have only a slow rate of loss of water, e.g. most sandhill species, many weevils and a few water-beetles. It is possible that certain xerophile beetles may possess the power of surviving a certain amount of desiccation better than do other beetles, and of recovering when conditions become damp again.

221. Fisher, R. C. (1938). "Studies of the biology of the death-watch beetle, *Xestobium rufovillosum* De G. II. The habits of the adult with special reference to the factors affecting oviposition." Ann. Appl. Biol. 25: 155–80.

Life of adult, egg laying and hatching. Times of pupation and emergence in the natural habitat, i.e. decayed parts of willow compared with those in buildings. "Indices of suitability" for various combinations of temperature and humidity in relation to egg-laying and hatching are calculated from experimental data.

222. Forestry Commission (1938). "Elm disease. *Ophiostoma ulmi* (Syn. *Ceratostomella* (*Graphium*) *ulmi*)." Leaflet No. 19, pp. 8. (Originally published December 1928; last revised February 1938. Forestry Commission, 9 Savile Row, London, W. 1.)

In this disease, caused by a fungus, the crown of the tree and the ends of the branches wither and lose their leaves, and the tree may die in one to several years, though the proportion killed is small. Two bark beetles (*Scolytus destructor* and *S. multistriatus*) make their breeding galleries under the bark, and those adults emerging before July are probably the most important carriers of the fungus. The disease apparently acts by the fructifications interfering with the flow of moisture through the woody tissues. Since it was first noticed in 1927 the disease has spread over a large area, south of the Scottish Border. A map shows it to be more frequent in the southern half of England (especially in the east) than in the north, in Wales or in Devon and Cornwall.

223. Hendrick, J., Moore, W. & Morison, G. D. (1938). "Activity of the sheep tick." Nature, Lond., 141: 648.

Ixodes ricinus appeared to be active throughout the year in north-east Scotland, seasonal incidence being highest in the summer and lowest in the winter. This finding disagrees with previous observation that activity is confined to spring and autumn periods.

4. PARASITES

See also **174, 185, 190, 215, 216, 223, 259**

224. Thompson, G. B. (1938). "The parasites of British birds and mammals. 18. The mammal-fleas and their hosts." Ent. Mon. Mag. 74: 109–13.

Analysis of the hosts of British mammal-fleas.

225. Thompson, G. B. (1938). "The parasites of British birds and mammals. 19. Further records of *Ornithomyia* spp. from British birds, together with notes." Ent. Mon. Mag. 74: 129–33.

226. Craufurd-Benson, H. J. (1938). "Bionomics of a cattle louse." Nature, Lond., 141: 921.

The apparently high incidence of infestation of dairy shorthorns in Hertfordshire with *Solenopotes capillatus*, and the occurrence of this louse also on cattle in Perthshire and Dumfriesshire, suggests a wider distribution and a greater importance than has hitherto been recognized.

227. Taylor, E. (1938). "Some records of bred Tachinidae (Diptera)." J. Soc. Brit. Ent. 1: 221–3.

Chiefly from Lepidopterous hosts, but some from woodlice.

228. Wilkinson, D. S. (1938). "On the identity of *Apanteles circumscriptus* Nees (Hym., Braconidae)." Proc. R. Ent. Soc. Lond. B, 7: 41–51.

Account of a single species of Hymenopterous parasite, with description, figures, discussion of synonomy, records of distribution and a detailed examination of host records.

229. Edwards, F. W. (1937). "The hosts of *Pterobosca paludis* Macfie." Ent. Mon. Mag. 73: 164.

Enallagma cyathigerum, Coenagrion pulchellum, Ischnura elegans, Libellula quadrimaculata and *Brachytron pratense* (all dragonflies).

230. Musgrave, A. J. & Mackinnon, D. L. (1938). "Infection of *Plodia interpunctella* (Hb.) (Lepidoptera, Phycitidae) with a Schizogregarine, *Mattesia dispora* Naville." Proc. R. Ent. Soc. Lond. A, 13: 89–90.

The parasite is a highly pathogenic Schizogregarine found in the fat-body and haemocoele of the larvae, pupae and adults of this moth. It is possible that the larvae are infected by ingesting the spores in contaminated food.

5. FOOD AND FOOD-HABITS

See also **145, 172, 251, 256, 261**

231. Berry, J. (1938). "The longtailed field mouse (*Apodemus sylvaticus*) as a destroyer of salmon ova." Avon Biol. Res. No. 5, 1936–37: 67–9.

Nest of this species in a hatchery box contained ova, and a mouse was seen to remove from water and eat one.

232. Braid, K. W. (1936). "Poisonous plants with special reference to the poisonous properties of bracken (*Pteridium aquilinum*)." Scot. J. Agric. 19: 247–51.

Species poisonous to stock in Scotland include yew (*Taxus baccata*), water dropwort or water hemlock (*Oenanthe crocata*), ragwort (*Senecio jacobaea*), and bracken. Experiments and observations proved that bracken can poison (often fatally) horses and cattle, but probably does not affect sheep much.

233. Bisset, N. & Rees, J. (1937). "Poisoning by ragwort." Welsh J. Agric. 13: 321–5.

Three small outbreaks killing cattle in South Wales. Although the cinnabar moth is very abundant, there seems little prospect of it controlling ragwort in this region.

234. Currie, P. W. E. (1938). "Notes on the association of thrushes and hawfinches." London Nat. for 1937: 87–8.

Hawfinches eating remains of yew berries rejected after being partly digested by mistle thrushes in a beech-yew wood on the Surrey Downs. The finches were seen to associate with the mistle thrush flocks at this time.

235. Buckstone, A. A. W. (1938). "Fish attacked by dragonfly larva." Entomologist, 71: 128.

Six-inch roach with a large dragonfly larva attached to one of its gills.

236. Dallman, A. A. (1937). "The pollination of *Picris echioides* L." North Western Nat. 12: 403–4.

A list of insects (six flies) visiting flowers.

237. Dallman, A. A. (1937). "Notes on the Hole of Horcum, Saltersgate, North Yorkshire. 5. The pollination of *Cornus suecica* L." North Western Nat. 12: 388–9.

A list of insects (two beetles, seven flies, and one moth) visiting this local plant.

238. Carpenter, G. D. Hale (1938). "*Arctia plantaginis* Linn. (Lep.) eaten by swifts." J. Soc. Brit. Ent. 1: 213–14.

This moth was abundant at the time and was being extensively preyed upon. For other records of the food of birds, see *id., ibid.*: 214 and **R. Cottam**, *ibid.* 235–6.

239. Morley, A. M. (1938). "More ravages of clothes moths." Entomologist, 71: 43–4.

Acompsia pseudospretella larvae feeding on the pupae of *Nyssia lapponaria* and *N. zonaria* in a garage.

240. Buckstone, A. A. W. (1938). "*Pieris rapae* a cannibal." Entomologist, 71: 34.

P. rapae devouring larvae of *P. brassicae.*

241. Hopf, H. S. (1938). "Investigations into the nutrition of the ash-bark beetle, *Hylesinus fraxini* Panz." Ann. Appl. Biol. 25: 390–405.

Food relations based on investigations into the enzymes of the alimentary canal and a comparative analysis of ash bark and frass of the beetle.

242. Freeman, P. (1938). "Notes on the nesting of five species of solitary wasps (Hymenoptera, Sphecoidea)." Proc. R. Ent. Soc. Lond. A, 13: 1–6.

Rhopalium clavipes, Psenulus atratus, Trypoxylon figulus, T. clavicerum and *T. attenuatum* were observed nesting in the straws of a thatched summer-house during the summer of 1936 at Slough, Bucks. When a wasp was seen going into a straw, the end of the straw was pinched between finger and thumb and the straw pulled out. The adult was kept for reference, measurements of the cells and counts of the prey were made, the prey was preserved in 70% alcohol and eventually identified. The prey of the first two species consisted of Psocoptera and Aphididae respectively and of the last three immature spiders.

6. POPULATIONS

See also **144, 145, 162, 185, 186, 210, 280, 282, 284, 286, 287**

243. Johnston, F. J. (1938). "The grey squirrel in Epping Forest." London Nat. for 1937: 94–9.

This area remained uncolonized until a late date (1935) since when grey squirrels have been destroyed as much as possible. One definite almost fatal attack of a grey upon a red squirrel observed. Other fresh-killed red squirrels were found, though there was no proof that grey squirrels had killed them. There was decrease in red squirrels after the arrival of the grey.

244. Gethin, R. G. (1936). "Pine marten visitor." Irish Nat. J. 6: 145–6.

Pine martens have been preserved at Curraghmore (the Marquess of Waterford's estate) during the last 35 years, and have increased a good deal, but keep chiefly to the woods.

245. Southern, H. N. (1938). "Isle of May breeding census." Scot. Nat.: 1–2.

Summary of investigation described in J. Anim. Ecol. (1938) 7: 144–54. (See **185.**)

246. Bletchly, J. D. (1938). "Some observations on the breeding-habits of birds." Brit. Birds, 32: 8–12.

Data on the incubation and fledging periods (and mortality rates) of birds in a mixed cultivated and woodland area in Gloucestershire, in 1930–33.

247. Wild, S. V. (1937). "A census of singing birds." (1937). North Western Nat. 12: 143–51.

A census of singing yellow buntings in 1935–36 on an area of two to three acres. In the second year the other birds were also included (ten species).

248. Venables, L. S. V. (1938). "Birds seen in two winter transects of the North Atlantic." Brit. Birds, 31: 295–6.

The commonest bird was kittiwake. These appear to be more numerous in winter, when fulmars and great shearwaters decrease.

249. Mitchell, M. (1938). "The rook (*Corvus frugilegus*) population of North-west Denbighshire." J. Anim. Ecol. 7: 20–1.

Nest density on about 113 sq. miles was about 14. Habitat preferences are analysed: no nests occurred above 600 ft.

250. Ward, J. H. (1936). "Rook roosts in the Manchester area." Naturalist: 153–6.

Roosting at various points, from about July to March. Notes on feeding grounds and flight lines.

251. Moeran, D. M. (1937). "Ravens in Co. Donegal." Irish Nat. J. 6: 155–6.

Great abundance of ravens in wild hill country attributed to epidemic among sheep said to be due to blowfly, and consequent large amount of carrion.

252. Duncan, A. B. (1938). "The magpie in Scotland." Scot. Nat.: 65–79.

References cover a period of 90 years, during which time it has steadily decreased. With the present break-up of large estates, magpies will probably tend to increase. Distribution records are given according to counties. The magpie is not found in Orkneys, Shetlands or Hebrides.

253. Longfield, C. (1938). "Observations on a colony of house martins, 1929–1935." London Nat. for 1937: 89–91.

Observations on a colony in a limestone cliff on the coast of County Cork, Eire, with notes on fluctuation in population (between ten and two pairs at limits), habits in nest-building, etc.

254. Nicholson, E. M. (1938). "Publication of the British Trust for Ornithology. The index of heron population, 1937." Brit. Birds, 31: 341–4.

A very large series of sample counts was made, covering about half the total breeding heron population. Comparisons with previous years, partly recalculated on a revised basis, show that extremely little change has taken place in the British Isles as a whole, though local changes are quite large. The result suggests an ability of the population to adjust itself as a whole.

255. Booth, H. B. (1936). "Fulmar petrels nesting on the Farne Islands." Naturalist: 199.

One pair nested, for first time, in 1935. In 1936 there were four birds incubating.

256. Stewart, M. (1938). "Notes on the gannetries of Sule Stack and Sula Sgeir." Brit. Birds, 31: 282–94.

There is a brief account of these two small islets, which lie north and north-west of Scotland (east and west of North Rona), and a history of work on their gannet populations. In spite of certain technical difficulties a rough estimate was made of the numbers: in 1937, about 3500 breeding pairs on Sule Stack and about 4500 on Sula Sgeir. There has been decrease on the latter, attributed to removal for food of large numbers of nestlings by men from Ness, in the Isle of Lewis. There is at present no legal means of preventing this destruction after 1 August.

257. Slack, H. D. (1937). "Notes on the viability of *Bacillus salmonicida* Emmerich and Weibel." Ann. Appl. Biol. 24: 665–72.

258. Cowley, J. (1938). "Quantitative methods of local entomofaunistic survey." Entomologist, 71: 8–12.

Notes on Valle's scheme for quantitative survey work as well as the marking methods of Borror, Swynnerton and Fletcher. Jackson's formula for estimating the total population from the recovery index and Balfour-Browne's estimation of the relative degree of concentration of a species in its different habitats are also mentioned.

259. Morison, G. D. (1937). "Some results of trapping the sheep blowfly (*Lucilia sericata* Meigen)." Scot. J. Agric. 20: 123–34.

This is the chief species responsible for "striking" sheep in Great Britain. A standard baited trap was used to study population distribution and numbers. 152,815 flies were trapped at different stations near Aberdeen in 1933–34, for periods varying from 39 to 165 days. Of these 6039 were *L. sericata*. The results are discussed in relation to habitat and weather, but the conclusions are not easily summarized. Notes are given also on other species of flies, on baits, and there is a useful bibliography, much of which concerns the blowfly problem in Australia.

260. Jones, D. P. (1936). "Gall midges affecting grass seed production in mid-Wales." Welsh J. Agric. 12: 192–7.

Five grasses of importance in Wales are affected by gall-flies, of which the species and their host-plants are discussed. The loss to the seed crop of grass is sometimes considerable.

261. Fenton, E. Wyllie (1937). "Biological notes for 1936." Scot. J. Agric. 20: 63–7.

Among other topics records serious damage to heather on certain moors in the west of Scotland, through heather beetle (*Lochmaea suturalis*), possibly also due to a fungus disease. There is also a discussion of the ecology of bracken, and the relation of its spread to reduction of cattle grazing. The house sparrow is pilloried as a pest.

262. Braid, K. W. & Tervet, I. W. (1937). "Certain botanical aspects of the dying-out of heather (*Calluna vulgaris* Hull.)." Scot. J. Agric. 20: 365–72.

In a discussion of the increase of bracken at the expense of heather on Scottish hills, it is suggested that although heather beetle and frosts are responsible for much heather destruction, there are also other factors such as fungus disease to be taken into account. A scale insect (*Lepidosaphis ulmi*) may also damage tissue. The ecology and distribution of certain fungi on heather are described.

263. Beak, T. W. (1938). "Investigation of the fauna of a water meadow carrier." Avon Biol. Res. No. 5, 1936–37: 29–41.

Bottom collections with a grab in a stream for seven months, provided figures for quantitative estimation of fauna in four different types of bottom. Seasonal variations are noted.

264. Beak, T. W. (1938). "Methods of making and sorting collections for an ecological study of a stream." Avon Biol. Res. No. 5, 1936–37: 42–6.

Discusses methods of taking bottom samples; also a new way of sorting samples, being an adaptation of Liddle's apparatus for sorting out animals from soil by means of high density liquids.

265. Stephen, A. C. (1938). "Production of large broods in certain marine Lamellibranchs with a possible relation to weather conditions." J. Anim. Ecol. 7: 130–43.

Sample counts of populations of two molluscs, *Tellina tenuis* and *T. fabula*, in the intertidal zone in the Clyde Basin were done from 1926 to 1937, and a marked fluctuation in the abundance of young was found, with peaks every three or four years: 1926, 1930, 1933, 1936 and 1926, 1930, 1933, 1935, respectively. This fluctuation is compared with meteorological factors (sun, rain and temperature) and a provisional correlation made between high "spat" years and high temperature. Tables of the size distribution of the two species in the samples in each year are given.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **162, 183, 211, 212, 217, 218, 255, 280, 281**

266. Leach, E. P. (1938). "Recovery of marked birds." Brit. Birds, 31: 302–8, 322–9.

267. Southern, H. N. (1938). "The spring migration of the swallow over Europe." Brit. Birds, 32: 4–7.

The average arrival dates of swallows in Europe are mapped with reference to movements of the 48° F. isotherm for the same period. A provisional correlation is made.

268. Thomson, A. Landsborough (1938). "A Publication of the British Trust for Ornithology. Report of the Bird-ringing Committee: progress for 1937." Brit. Birds, 31: 345–51.

The bird-ringing scheme, carried out since 1909 under the auspices of "British Birds", has passed to the control of the Trust, with headquarters for this section of its research, at the British Museum (Natural History). In 1937, 21,900 birds were trapped and ringed, and 23,281 nestlings: total, 45,181 birds. Details are given of numbers ringed by different observers, the numbers of each species ringed in 1909–36, and in 1937, and the percentage recovered of those ringed in 1909–36.

269. Lack, D. & Lockley, R. M. (1938). "Skokholm Bird Observatory homing experiments. 1. 1936–37. Puffins, storm-petrels and Manx shearwaters." Brit. Birds, 31: 242–8.

Some preliminary results of ringing birds of which the results are difficult to summarize. The authors state that "at this stage the experimental data do not warrant further discussion". One Manx shearwater taken to Venice (930 miles away) and released on 10 July 1937 was recovered on Skokholm (S.W. Wales) on 24 July 1937. If the bird came back by sea it must have gone at least 3700 miles. Venice is outside the known range of the species. Other birds released in Ireland, Scotland, Faeroes, and places inland in England, were also recovered. The number of shearwaters originally ringed is not stated. There is a short but useful list of references to foreign investigations on homing.

270. Moreau, R. E. (1937). "Migrant birds in Tanganyika Territory." Tanganyika Notes & Records, No. 4.

Contains, as well as a survey of tropical migration, a valuable section on Palaearctic migrants in their winter quarters with a summary of what is so far known of distribution, habitat selection in comparison with summer quarters, condition of gonads prior to spring migration, incidence of moults and records of singing.

271. Temperley, G. W. (1938). "Ornithological report for Northumberland and Durham for the year, 1937." Vasculum, 24: 55–9.

Discusses the weather and its effect on bird movements. Gives distributional, abundance, nesting and other notes.

272. Dannreuther, T. (1938). "Migration records, 1937." Entomologist, 71: 60–6.

A general summary for the year.

273. Garrett, F. C. (1938). "Migrant Lepidoptera in 1937." Vasculum, 24: 19–20.

Some northern records.

274. Grant, Mrs K. (1938). "A migration of cabbage white butterflies in Hertfordshire in May, 1937." Entomologist, 71: 103–7.

275. Maldwyn Davies, W. & Whitehead, T. (1938). "Studies on aphides infesting the potato crop. VI. Aphis infestation of isolated plants." Ann. Appl. Biol. 25: 122–42.

Winged aphides had no difficulty in detecting and colonizing isolated plants which can be reached from a distance of at least a quarter of a mile.

276. Stephen, A. C. (1938). "Temperature and the incidence of certain species in Western European waters in 1932–34." J. Anim. Ecol. 7: 125–9.

Accompanying the unusually high temperatures in the Atlantic in 1932–34, a good many animals from more southern waters were found in abnormal frequency round the British Isles. These animals include whales and dolphins, fish, tunicates, pelagic molluscs and cirripedes, siphonophores and Protozoa. Attention is also drawn to certain other phenomena, including the disease in eel-grass (*Zostera*), unusually great appearance of the young of certain fish and molluscs, and unusual local abundance of certain British species.

277. Storrow, B. (1938). "Faunistic and hydrographic changes." Nature, Lond., 141: 798–9.

The recent occurrence of seven species of fish and one species of crab not usually found on the Northumberland coast is explained by the established abnormal activity of Atlantic water around the north of Scotland, followed by a southern movement of colder Norwegian water driving the animals south into the North Sea.

278. Stelfox, A. W. (1936). "*Physalia*, 'the Portuguese man-of-war', and *Velella* in Irish waters." Irish Nat. J. 6: 142–3.

Velella sp. seen in Bantry Bay in July 1935. This siphonophore is not infrequent in some years; but *Physalia* is very rare and has not been definitely recorded for a hundred years, although in exceptional years it is seen off the south-west coast of England.

279. Forrest, J. E. (1938). "*Velella spirans* (Forskal) in the Outer Hebrides." Scot. Nat.: 10.

This siphonophore appeared in fair abundance off the island of Barra in July 1937.

8. REPORTS OF ORGANIZATIONS

280. British Trust for Ornithology (1938). Fourth Report, Summer 1938. 33 pp.

Arrangements have now been made to set up the Edward Grey Institute of Field Ornithology in Oxford, to provide better facilities for bureau work and a research centre. The "British Birds" bird-ringing scheme has been transferred into the control of the Trust, with headquarters in the British Museum (Natural History). Investigations include the little owl enquiry (whose report was reviewed in J. Anim. Ecol. (1938) 7: 161–2); woodcock distribution and ecology; woodland bird distribution; song periods; lapwing habitats; sample heronry census covering a large part of the country, certain habitat and distribution enquiries through local natural history societies (magpie, coot and red-backed shrike). New enquiries being started include survey of black-headed gull breeding colonies; corncrake distribution; bridled guillemot varieties. Local bird census work round Oxford was continued. The work of this organization is expanding steadily, as is the support given to it by ornithologists.

281. Skokholm Bird Observatory (1937). Report for 1937. 22 pp.

The Observatory was started in 1936, and is run by R. M. Lockley in co-operation with various observers and organizations. In 1937 there were over a hundred observers, not counting day visitors; 4404 birds were ringed (2059 as adults), also 1797 Manx shearwaters in a special investigation on homing. The figures for census of breeding birds over ten years are given. The neighbouring island of Grassholm has, through the action of its proprietor, been placed partly under control of the Observatory for bird watching, and activities such as gannet ringing. A number of migration notes, etc., are included, also parasite records, and information about grey seals, Soay sheep, and rabbits. In 1936 and 1937 a virus disease, myxomatosis, was introduced with the aim of controlling rabbit numbers. The numbers in 1936 were estimated at about 20–25 per acre. Although the disease spread to a certain extent, it did not appreciably decrease the population, and it is thought the virus has died out. There is a large population also of house mice (*Mus musculus*) introduced thirty years ago, living all the year round out of doors. There are a few notes on butterfly migrants and on plants, in particular bracken, which is said to favour increase in gulls by providing nesting cover. The effect of bracken on various birds is summarized.

282. Bureau of Animal Population, University of Oxford (1937). Annual Report, 1936–37. 38 pp.

Reviews general position of population research in relation to human affairs; and the particular researches of the Bureau on vole populations (*Microtus agrestis*), game birds and animals, certain North American species (including the snowshoe rabbit, *Lepus americanus*, and the arctic fox *Alopex lagopus*), and special surveys including semi-wild animals at Whipsnade, squirrels on a Hampshire estate, habitats of mice and bank voles, moles; also introduced animals, including grey squirrels. Attention is specially given in these researches to the structure and fluctuations of the populations.

283. Lancashire and Cheshire Fauna Committee (1937). Twenty-third Annual Report and Report of the Recorders for 1936. 52 pp.

A valuable list of local records often with habitat notes, covering vertebrates, various insect groups, *Arachnida*, woodlice, non-marine Mollusca and plant-galls. The report gathers together a large amount of scattered information from many observers. There are also some ecological notes on selected species of birds: grey wagtail, lesser redpoll, and little owl. Notes include habitats at different seasons, nesting sites, and numbers.

284. Yorkshire Fishery District, Board of Conservators (1937). Seventy-first Annual Report on the salmon, trout and freshwater fisheries in Yorkshire. (By **W. T. Clarke.**) 47 pp.

Contains figures of the number and weight of salmon and migratory trout caught in river, estuary and sea (total 2425 salmon, weighing 35,198 lb.; 1788 migratory trout, weighing 6669 lb.), notes on coarse fish, fish passes to counteract the effect of dams and weirs, pollution (which is decreasing), and the recovery of marked salmon and trout.

285. West Riding of Yorkshire Rivers Board (1937). Forty-second Report, 1934–37. Wakefield, Yorkshire.

This report, though dealing mostly with administrative measures, gives a good idea of the intricate relations between the various interests using rivers: water-supply, sewage, industrial effluents, land drainage, fisheries, etc. The main subject dealt with is sewage and effluent disposal, but it is pointed out that pollution is now less an obstacle to salmon entering the Yorkshire rivers (which they still do in some numbers), than the large amount of yellow alluvial silt in suspension in tidal waters, and the construction of impassable weirs and dams. The Board claims that pollution is now being dealt with more and more effectively at the sources. The clean rivers, Ure, Nidd, Wharfe, Aire (part), Ouse and Ribble (West Riding reaches) "have all remained in good condition and are well-stocked with fish". Chemical and water-flow data for some rivers are given.

286. Avon Biological Research (1938). Annual Report, No. 5, 1936–37. 80 pp. (University College, Southampton. Price 2*s.* 6*d.*)

The research deals mainly with salmon and trout in the River Avon, but takes a wide view of the environment and of other species of animals. Some separate papers in the Report are noticed elsewhere.

287. Freshwater Biological Association of the British Empire (1938). Sixth Annual Report, for the year ending March 31st, 1938. 73 pp.

The work of this organization, with laboratory at Windermere, is mainly pure research with a bearing upon economic problems such as freshwater fisheries and water supply. The investigations around Windermere embrace a wide scope, including the physical conditions and vegetation, and also surveys of animal ecology, among which are: the relation of lake bottom deposits and physiographical history of Windermere to the flora and fauna; the distribution of invertebrate animals in the Lake District (mainly with reference to Mollusca and insects); and population studies of salmon, etc. The Association appears to be extending its membership widely among biologists, fishery organizations and water-supply undertakings.

288. Marine Biological Station at Port Erin, Isle of Man (1937). Report for 1937 (No. 50). 24 pp.

Includes notes on oyster culture experiments, and a list of corrections and additions to Moore's "Marine Fauna of the Isle of Man" (see Notice No. **143**).

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